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NOTES ON THE RADULA OF THE HELICINIDAE.

By H. Burrington Baker.

This paper is the result of an attempt to ascertain the generic position of three species of Helicinidae, which were collected by the University of Michigan-Walker Expedition in Southern Vera Cruz, Mexico (1910). This led to the examination of the type species of characteristic examples of many of the groups of North American Helicinidae. The majority of the radulae was studied from alcoholic or dried material in the collection of The Academy of Natural Sciences of Philadelphia, kindly put at my disposal by Dr. H. A. Pilsbry, whose advice and criticism were of invaluable assistance. I am indebted to Mr. E. G. Vanatta and Dr. C. M. Cooke for help, especially in technique. Mr. John B. Henderson also sent me several Cuban species from his own collection.

Three of the species were studied from the University of Michigan collection from Mexico, to which reference has just been made, while additional material came from a collection made in Venezuela in 1920. As the study was attempted in order to arrange Mexican forms, a synopsis of the North American mainland species is included in the notes on each group. I hope to take up the species from northern South America in a future paper.

A. J. Wagner (1905, 1907–1911) made the most thorough attempt, in recent times, to arrange the species of Helicinidae. His classification is based solely on shell-characters, mainly the shape of the operculum and the position of its nucleus. Although a great advance on earlier attempts, his work is seriously marred by a general disregard of previous writers on the subject, and of the modern laws of priority. Of the 36 new group-names, proposed by him for American Helicinidae, only about 16 can be used.

The embryonic operculum of the Helicinidae is spiral and its spiral nucleus is evident in the adults. Thus the adult operculum may perhaps be regarded as potentially spiral, with the rotation arrested by the shape of the aperture. The microscopic structure of the columellar margin of many species certainly adds to this impression, as the growth-lamellae are crushed and bent outwards in this region, as if they actually had resisted an attempted torsion. The position of this thickened region varies with the shape of the aperture.

The operculum consists of two quite distinct layers, an inner horny layer, which is often lacking in dried specimens, and an outer, calcareous one. The horny layer shows the growth-lamellae and the spiral nucleus much less distinctly than does the calcareous portion. The relative development of these two layers gives an additional character, little used by Wagner.

The radula of the family has been variously described and figured but, in most cases, neither figures or descriptions are very usable. Under low magnification, it appears to consist of a narrow, transparent trough, with a broader, rounded ridge on each side. It is long and narrow, and in most of the species observed by me, consists of about 100 transverse rows, although the extremes show from 80 to 171. This character seems to be mainly dependent on size, and is of little value in the determination of relationships.

Under higher magnification, five groups of teeth can be made out: a central group; and a lateral or capituliform complex, and a marginal group on each side. The central group consists typically of seven, very small, almost colorless teeth (Plate III): the unpaired or rhachidian tooth and three paired centrals on each side. For brevity, in the following descriptions the unpaired central is termed the R-central (at the left hand in the figures), while the paired centrals are called the A-central, the B-central and the C-central, in order from the inside out (left to right in figures). The R-central is usually a thin and transparent plate, which is bent upwards at its distal end so as to form a broad scraping edge, or cusp. The paired centrals are variously shaped and cusped, but the A-central and B-central primitively appear more or less boot-shaped, while the C-central is usually more or less lanceolate in outline.

The lateral or capituliform complex consists of two structures, which are so closely united, as at first to give the impression of a single, large and complicated lateral (the capituliform lateral of Fischer, (1885.)) Closer examination shows this complex to consist of two pieces: a comb-shaped (or T-shaped in Vianinae) lateral and a variously modified, outer accessory plate. The comb-lateral, as it may be termed (Plate IV, fig. 17, left), is more or less trapezoidal or spoon-shaped as viewed from the central side, and the upper edge is thickened and reflected (Plate IV, fig. 17a). This upper edge is so heavy as to appear horn-colored, even under high magnification, and bears the large cusps. The outer, handle

like portion (Plate IV, fig. 17b) is continuous with a thickening on the central posterior side of the tooth; this thickening runs diagonally from the base to near the inner tip of the comb-lateral. Outside of the handle-like portion is a thinner, triangular portion portion (Plate IV, fig. 17c), which fits over the inner end of the accessory plate. The anterior (upper in figures) edge of this triangular portion is often thickened and reflected, so as to form a continuation (Plate IV, fig. 17d) of that which bears the cusps. On the under-side of the comb-lateral is a saddle-shaped depression or hole (Plate IV, fig. 17e) dotted lines, into which fits the base of the comb-lateral next anteriad.

The accessory plate (Plate IV, fig. 17, right) is a large, but usually thin and transparent, trapezoidal plate, externad to the comb-lateral. The inner end (Plate IV, 17f) fits under the triangular outer portion of the comb-lateral. In many species, all of the anterior edge, except that of the outer lanceolate appendix (Plate IV, 17g) is reflected to form a broad ledge (Plate IV, fig. 17h). This is often strengthened by thickenings of various shapes, and appears to form a support for the comb-lateral. In *Hendersonia* and *Oligyra*, this reflected portion appears to form a wing, which completely invests the base of the comb-lateral so as to mask its inner cusps. In many other genera, it is much reduced and only connects with the outer prolongation of the cusp-bearing portion. In the figures where the two pieces are shown separated, the position of the inner end of the accessory plate is marked by an (x) on the comb-lateral, while that of the outer extremity of the comb-lateral is marked on the accessory plate in the same manner.

The above description is based on the laterals of the Helicininae. In the group of species that center around the genus *Eutrochatella* (Vianinae), the capituliform complex is so highly modified as hardly to be recognizable. The accessory plate is much reduced, while the comb-lateral is represented by a large T-lateral. The latter is very much the shape of half of a mushroom. It bears a broad, reflected cusp, which is semicircular in outline as viewed from the anterior end, while the stalk portion is about at its middle. The accessory plate usually has a rather heavy anterior thickening which may form an inner hook, and fits over the outer branch of the stalk.

In the normal position, the accessory plate and the outer portion

of the comb-lateral are usually hidden by the overhanging marginals, even after the radula is flattened out. The centrals are arranged in a slightly convex line along the bottom of the trough, already mentioned, while the accessory plate is tilted slightly dorsad under the ends of the innermost marginals.

The marginal group consists of a varying number (28 to 136 in the species studied) of ligulate teeth. The number appears to vary with the size of the species; but a considerable variation in number, among species of similar size, appears to be a matter of systematic importance. These teeth or uncini are proportionately quite large and are so heavy as to appear horn-colored. They are arranged in very oblique rows, which run posteriad from the corresponding capituliform complex. The bases (Plate III, fig. 6, 9) are broadly U-shaped, with the open portion of the U facing the outside of the radula; those of contiguous teeth nest into one another. The body of the tooth is twisted so as to bring the cusps into action. These are arranged across the tip of the tooth or down its outer side. The innermost marginal (Plate III, fig. 9) is the broadest and shortest of the entire functional series. In the species observed the length usually increases gradually toward the outside of the radula, until the longest teeth are about one-third of the way out from the center; here the teeth are from 1.5 to 2 times as long as are the innermost. Towards the outer edge of the radula, they again decrease in length, so that the outer teeth are not much longer than the innermost. The distal portion becomes more slender in the teeth toward the outside, so that these may only be one-third as wide, near the tip, as those at the inner edge. However, the bases of the marginals are of about the same width throughout each transverse row, andthevery outermost teeth take the form of delicate, rectangular plates,as wide as the bases, and arranged almost parallel to the long axis of the radula. In all of the species observed, the inner marginals (except sometimes the innermost one or two) has the smallest number of cusps, while the number gradually increases towards the outside of the radula. Each new cusp in the series is added to the outside of the row of cusps. I have as high as 15 cusps on the outer, definitive teeth, and have estimated, by counting portions of the total row, that some of the broad, outermost marginals have at least 25. The cusps of these outer, scale-like teeth are so minute as to approach the limits of microscopic vision, which probably accounts for the statement

of Troschel (1856–63) that they are without cusps. In every species that I have examined under an oil-immersion lens, they could be detected.

Two lines of development appear in the structure of the marginals. The type that is here considered the most primitive is that represented by *Hendersonia*. In this and related groups (Table I), there are a comparatively small number of teeth ,with one or two major cusps and many minor ones arranged along the outside of the tip. In *Helicina* there is an evident tendency for the cusps to arrange themselves on the extreme tip of the tooth, while many West Indian genera show a tendency to accentuate the one or two major cusps. The climax of the first line of development is seen in *H. zephyrina*, where the cusps of each tooth form a nearly transverse row, with the largest teeth in the center of the terminal disc; each tooth is so twisted as to bring the transverse crown of cusps in a line nearly at right angles to the long axis of the radula. The other line of development finally results in the unicuspid inner marginals of *Stoastoma* and the Vianinae (*Trochatella*).

On account of their complexity, and the vertical position of the numerous marginals, the radulae of the Helicinidae are peculiarly difficult to study. For this reason it is often necessary to examine quite a few specimens and to view the teeth in every possible position, in order to correctly interpret their shape. The best results were obtained by cutting each radula transversely into several pieces with a rather dull-edged scalpel, so as to leave torn edges. Each piece must be carefully arranged and then the cover-glass dropped on suddenly to flatten the ribbon. In order to study the accessory plate it is absolutely necessary to get a place where the marginals are missing or turned back. Separated capituliform complexes are also of great aid, although the accessory plate, and especially the wing, is only too often broken in the process. If the centrals are separated from the laterals and marginals, the cover-glass usually flattens them into a position where it is very difficult to study them. In all cases, except that of *Helicina neritella*, the centrals, laterals, and the tips of the marginals, are shown in the figures as nearly as possible to the natural position, so as to make the views uniform.

When one becomes accustomed to the changes in apparent shape, due to different view points, the radulae of different specimens of the same species show remarkably little fluctuating variation. The centrals and laterals rarely show a variation of more than a

single cusp, although more commonly one or two cusps will be considerably reduced. However, the cusps of the centrals, laterals, and inner marginals are quite often broken or worn, so as to give an apparent variation, but an examination of all parts of the radula will easily remove this source of error. In specimens of similar size, the maximum variation in the number of marginals was 5 teeth, and part of this may have been due to the difficulty in ascertaining to which row the divergent outer teeth belonged. However, a dwarfed form of *Helicina adspersa* (*H. a. marmorata* d'Orb. + *tenuilabris* Pfr.) had only 80 marginals on each side, while the larger form had 106.

On the other hand, big variations are fairly common. In one of the radulae of *Lucidella aureola* and in one of *Oligyra orbiculata*, two rows of A-centrals were present on each side, so that there were 9 teeth in the central group; this, if a constant character, would exclude them from the *Helicinidae*, as at present defined. In these cases, the outer A-central was a little smaller than the inner, and, especially in the latter species, somewhat approached the B-central in shape. In another radula of *H. orbiculata*, all but one of the cusps on one row of A-centrals were absent or vestigial, although the other side was perfectly normal. In a radula of *Hendersonia occulta*, the seventh marginal on one side was vestigial, while an entire longitudinal row of marginals on the other side was branched, and bore from 2 to 4 quite perfect tips, each with its full complement of cusps. In a specimen of *Helicina adspersa marmorata*, most of the cusps were represented by mere knobs on one row of comb-laterals, although those of the other side were normal. However, this type of variation comes under the heading of monstrosities or mutations, and is very easily separated from fluctuating or intergrading variation. It does not affect the use of the radula as an index of relationship, any more than the presence of gill-slits, or a fuller complement of aortic arches in an adult human being, affect the use of these characters in the classification of vertebrates.

In the following arrangement of the groups of species from the mainland of North America, the radular characteristics are listed in some detail. Opercular and other shell characters are omitted unless used for the separation of groups; they are treated in detail by A. J. Wagner (1907–1911). In each case the name of the group is given first, followed by a list of synonyms. In the West Indian

groups, which were not studied in detail, sectional names are sometimes included as synonyms under subgenera or typical sections. Next comes a list of the species in each group from the mainland of North America, with synonomical notes, followed by a description of the radulae of examples studied.

The following synoptic key shows the main distinguishing characters of the groups studied:

A. Capituliform complex consisting of a comb-lateral and accessory plate..... Subfamily Helicininae.
  B. Operculum paucispiral; radula "like *Helicina*"..*Bourciera*.
  BB. Operculum subspiral to eccentric.
    C. Accessory plate with well-developed wing which invests the base of the comb-lateral so as to mask its outer cusps; all paired centrals with well-developed cusps; operculum with calcareous plate quite well-developed and forming a complete operculum; horny plate thin, usually amber-colored.
      D. Operculum subspiral to almost concentric; cusps of centrals very well-developed; cusps of comb-lateral exceptionally long and pointed; accessory plate short and heavy with triangular wing; marginals few (39–43).....*Hendersonia*.
        E. Operculum subspiral with marginal nucleus Sect. *Hendersonia* s. s.
        EE. Operculum subspiral with submarginal nucleus Sect. *Miluna*.
        EEE. Operculum almost concentric, with nearly central nucleus.....Sect. *Waldemaria*.
      DD. Operculum eccentric with nucleus near middle of columellar margin; cusps of C-central somewhat reduced; accessory plate longer; marginals more numerous (52–123).....*Oligyra*.
        F. A and B centrals not developing heavy backs; comb-lateral with few, sharp-pointed cusps (6–7); operculum light with point and corresponding lip-notch poorly developed Subgenus *Oligyra* s. s.
        G. A and B centrals like *Hendersonia*; accessory plate with wing slightly reduced, so as to show lanceolate outline;marginals quite strictly ligulate; shell depressed with heavy lip Section *Oligyra* s. s.
        GG. A-central with tendency to reduce the number of cusps, which are borne on the extreme outer tip; marginals with wing-like expansions below the tips, and with number

of cusps increasing rapidly towards outside; shell more globose..... Section *Succincta.*

FF. A and B centrals with heavy knob-like cusp-bearing backs; capituliform processes heavy and interlocking; marginals ligulate; operculum heavy and usually with inferior point, which fits into notch in lip..... Subgenus *Alcadia.*

H. Smallish shells with notch in lip less well-developed; comb-lateral with more pointed cusps..... Section *Idesa.*

HH. Larger shells with well-developed notch or lower lip of aperture; comb-lateral with large spatulate cusps; R-central longer than broad..... Section *Alcadia* s. s.

CC. Accessory plate smaller with reflection (slightly developed or absent) which at most only invests the outer tip of the prolongation of the thickened upper edge of the comb-lateral; centrals and opercula various.

J. A-central with cusps like *Oligyra*, or with a thickened, cuspless cutting edge; marginals with tendency for the numerous cusps of each tip to arrange themselves in a transverse row; operculum with calcareous plate poorly-developed, often incomplete towards palatal margin; horny plate well-developed and bright-colored, usually red *Helicina.*

K. Marginals sickle-shaped with well developed lateral wings near tips; A-central with shelf-like projection bearing the cusps; accessory plate with small body but large lanceolate appendix, and with the reflected anterior edge forming a rather prominent shelf; operculum and comb-laterals as in *Tristramia.* s. s Subgenus *Helicina.* s. s.

KK. Marginals quite strictly ligulate; A-central and accessory plate not as preceding Subgenus *Tristramia.*

L. All paired centrals with well-developed cusps; calcareous plate of operculum usually somewhat thickened above nucleus, opaque milky-white to bluish; shells usually with spiral striations

M. Comb-lateral with numerous (9–11), long, sharp cusps; shell depressed, angular to subangular..... Section *Oxyrhombus.*

MM. Comb-lateral with more rounded cusps (8–10); shell globose.... Section *Tamsiana.*

LL. A-central without well-developed cusps; with heavy edge.

N. A-central with one or two points on heavy cutting edge; comb-lateral with numerous rounded cusps; C-central with two rounded points and sometimes 1 or 2 smaller ones; operculum as in *Tristramia* s. s., depressed, angular shells, usually with well-marked spiral striations.....Section *Angulata.*

NN. A-central without cusps; comb-lateral with broad, spatulate cusps; operculum with calcareous plate thin, weak, and usually incomplete; globose shells, usually with poorly marked spiral striations

O. 4 cusps on C-central....Section *Tenuis.*

OO. One rounded hook on C-central Section *Tristramia.*

JJ. A-central *Alcadia*-like or highly modified; marginals with tendency to reduce number of cusps and to develop one or two primary ones, with others arranged along outer side; calcareous plate of operculum usually better developed than horny plate.

P. A-central hood-shaped; comb-lateral with long and pointed cusps; accessory plate large but thin.....*Lucidella.*

Q. A-central with well-developed cusps on margin; C-central without lateral cusp; shell with lip entire, perforate.....Subgenus *Lindsleya*??.

QQ. A-central without well-developed cusps on margin; C-central with accessory cusp on outside margin; shell imperforate; usually toothed

R. C-central long and slender; few cusps on comb-lateral (6); small species Subgenus *Poenia.*

RR. C-central broadly lanceolate; many cusps on comb-lateral (9–10); larger species Subgenus *Lucidella.*

PP. A-centrals not hood-shaped; comb-lateral with spatulate or very few (3) cusps; accessory plate smaller, but usually heavy.

S. Paired centrals *Alcadia*-like; comb-lateral heavy with at least 6 cusps; inner marginals bicuspid.....*Schasicheila.*

T. Only few (1–4) marginals bicuspid; shells heavy, *Analcadia*-like; Western Cuba Subgenus *Emoda.*

TT. More (9) marginals bicuspid, close-ranked; shell usually with upper sinus on aperture; Mexico and Guatemala
Subgenus *Schasicheila.*

SS. A-central unicuspid; B-central with 3 heavy cusps; comb-lateral tricuspid; inner 10 marginals unicuspid; shell small, slightly like *Schasicheila* s. s. in shape.....*Stoastoma.*

AA. Capituliform complex consisting of a mushroom-shaped T. lateral and a reduced accessory plate; many unicuspid marginals.....Subfamily Vianinae, new.

B. Marginals with sharp-pointed blades; T-lateral with stalk as long as width of tooth, which is considerably smaller than central field of radula; R-central triangular-ovoid to broadly elliptic.....*Eutrochatella.*

C. All paired centrals with at least three well-developed, cusps; T-lateral with cusps on margin; shells smallish quite smooth and elongate
Subgenus *Troschelviana,* new.

D. T-lateral with well-developed cusps on inner portion of margin; shell smallish, quite smooth and elongate:
Section *Troschelviana.*

DD. T-lateral with a few cusps towards outer portion of margin: shell more conoid in shape
Section *Cubaviana,* new.

CC. At least A-central without well-developed cusps; T-lateral without cusps on margin; shell with spiral sculpture.

E. B-central with 3 quite well-marked cusps; T-lateral with horny thickenings near margin which give the tooth a wavy appearance; small species
Subgenus *Pyrgodomus.*

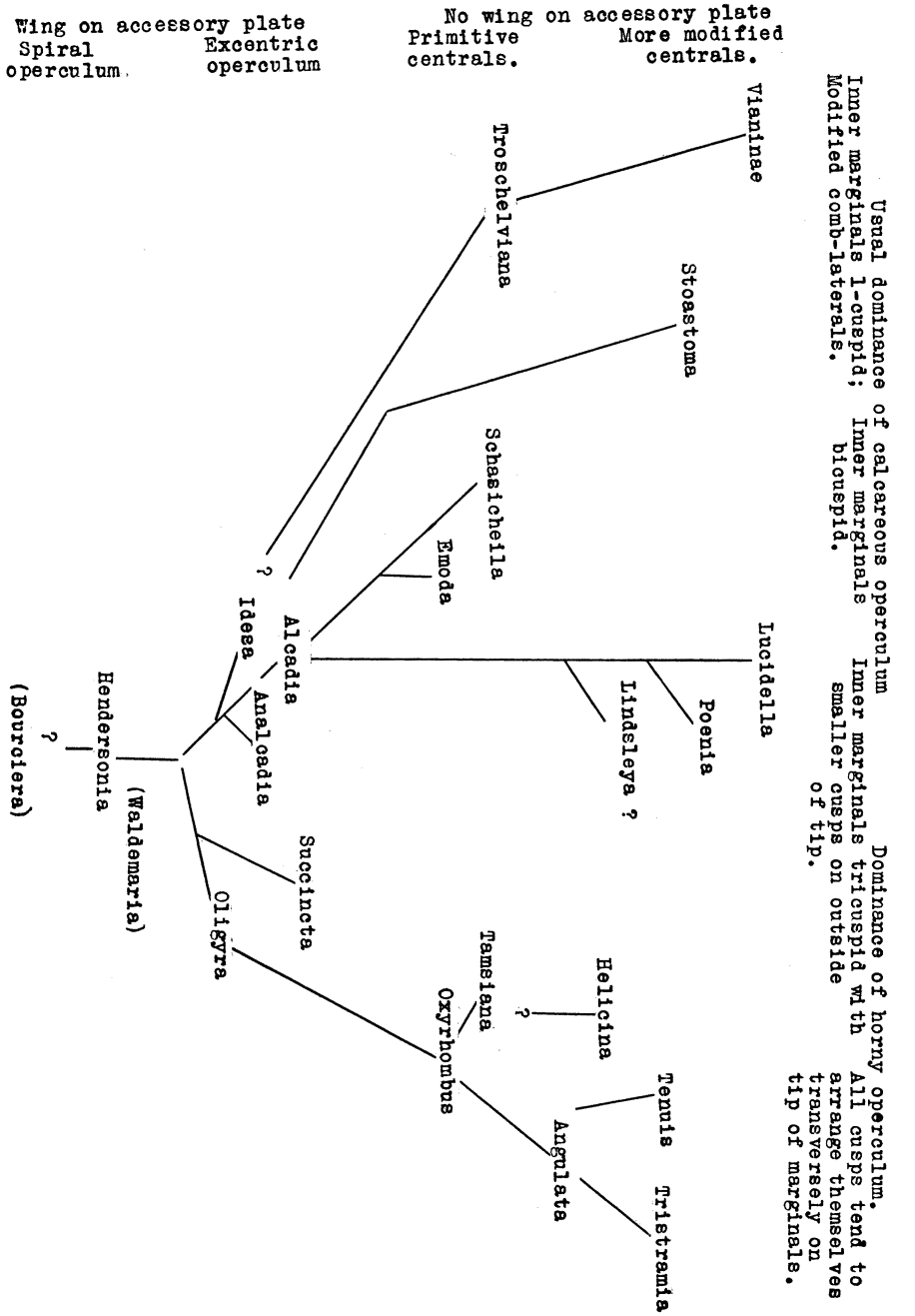
EE. Both A and B centrals without well-marked cusps; T-lateral without sign of cusps; larger species.

F. R-central broadly elliptic; operculum with nucleus near columellar margin and almost linear; depressed pagoda-shaped shell
Subgenus *Priotrochatella.*

FF. R-central narrowly ovoid to circular; operculum with nucleus nearer center
Subgenus *Eutrochatella;* Sections *Ustronia, Excavata, Eutrochatella.*

BB. Marginals with tips more rounded; T-lateral with short, stout stalk, and broad, semicircular cutting edge, so that entire tooth is almost or fully as large as the central field of the radula (7 teeth); R-central more or less shield-shaped with scallops on lateral margins; paired centrals and T-lateral without cusps.

TABLE I. RELATIONS OF HELICINID GROUPS.



G. A-central very large; B and C centrals especially reduced; many marginals (100) with rather long blades; R-central with rounded base; shell large, globose, that of male with a sinus on outer lip; operculum with heavy calcareous plate..... *Viana.* Cuba.

GG. All paired centrals more nearly uniform in size; few marginals (28) with short, broad blades; shell depressed, angular; operculum linear, with horny plate dominant..... *Calybium.* Indo-China.

H. Shell with columellar folds, radula unknown
Subgenus *Calybium* s. s.

HH. Shell without columellar folds; radula as above
Subgenus *Geotrochatella.*

Genus **BOURCIERA** Pfr. Ecuador.

Bourciera Pfr. (1851). Type *B. helicinaeformis* Pfr. (1851).
Bourcieria auct., not of Bonaparte (1850), in birds.
Pseudhelicina Sykes (1907). Proposed new name for *Bourcieria* auct.; not Pfr.

Bourciera, omitted from Wagner, has a paucispiral operculum. Troschel (1856–63) describes and figures the radula of the type species and remarks: "In regard to the structure of the radula, the genus *Bourciera* belongs to the Rhipidoglossa, and indeed to the family Helicinacea; in fact it agrees so with *Helicina* itself, that a difference in the dentition can hardly be stated" (translation). His figure does not show definitely the structure of the capituliform complex, which I regard as especially important in the determination of relationships, but the centrals and marginals appear quite similar to those of *Hendersonia*, and I believe the two groups will be found to be quite closely related. There can be no doubt of its position in the Helicinidae.

Unless the structure of the operculum is secondary, this is probably the most primitive member of the family. As it is the only genus confined to South America, and none of the other genera appear to have developed very distinct groups on this continent, it seems as if all of the South American Helicinidae are probably quite recent immigrants from the north and that *Bourciera*, like the llama amongst the mammals, is a survival, in the Andes of Ecuador, of a primitive type, which disappeared from its original nearctic or holarctic home after its invasion of this new territory.

This idea is further substantiated by the total absence of the Helicinidae from Africa and the paucity and Oriental type of the Australian species. Probably it is safe to state that the Helicinidae

were absent from the ancient Atlantic or Antarctic continents, or, if present, have left no modern descendants.

Genus **HENDERSONIA** A. J. W. United States, China, Japan.

Apiopomatinae A. J. Wagner (1905). No possible type genus.

Section HENDERSONIA s. s. United States

Hendersonia A. J. Wagner (1905). Type (monotype) *Helicina occulta* Say (1831). Subfossil, New Harmony, Indiana.

H. occulta (Say) (1831). Subfossil, New Harmony, Indiana. (North-eastern U. S.). *H. rubella* Green (1832). Alleghany County, Pa., U. S. (living or fresh).

Section MILUNA A. J, W. S. China.

Miluna A. J. W. (1905). Type (monotype) *M. josefinae* A. J. W. (1905); Radung-Hubei.

Section WALDEMARIA A. J. W. Japan.

Waldemaria A. J. W. (1905). Type *H. japonica* A. Adams (1861). Japan.

In this genus the radulae of *H. occulta* (Say)[1] and *H. japonica* (Adams)[2] were examined. The formulae are shown in Table II. In this table, under the headings "A, B and C Centrals" (the R-centrals are omitted as they usually have no true cusps) are given the number of cusps on each tooth for the various species. Under the heading "Comb-lateral" are given the number of cusps on that tooth. Under the heading "Marginals," the subheadings "2, 3, 4, 5, 6" indicate numbers of cusps; under each of these subheadings is given the number of teeth that bear the complement of cusps indicated. Where the inner teeth bear more cusps than some further out; these interstitial few-cusped teeth are put in their proper column but are marked with an asterisk, while the two groups of teeth with one more cusp, situated on either side of them, are put in their proper column but the first and second groups are separated by a plus sign. For instance, *A. verecunda* has 4 cusps on the inner most marginal (1 in 4-column), followed by 2 teeth with 3 cusps each (2 followed by an asterisk in 3-column), which in turn are followed by 3 more teeth with 4 cusps (+ 4 in 4-column). Under the heading "Total" are given the number of marginals on each side; under "Grand Total" are given the usual number of teeth in each transverse row.

In *H. occulta*, the R-central (Plate III, fig. 1) is peculiarly attenu-

[1] 5 dried specimens; A. N. S. P. no. 10593; collected at Iowa City, Iowa, by B. Shimek (1891), and H. A. Pilsbry (1882).

[2] 2 dried specimens; A. N. S. P. no. 84383; collected at Sotokaifui, Sado, Japan, by Y. Hirase (1902).

ate basally. As remarked in the key to the groups, the cusps of the paired centrals, and especially those of the C-central, are larger and better-developed than in any other group; in fact the whole central group is large in comparison with the rest of the radula. The comb-lateral has comparatively few cusps, but these are large, and exceptionally long and well-pointed (Plate IV, fig. 10). The accessory plate is heavy but short, and has horn-colored thickenings along the inner end and down the middle, while in most of the nearly related groups it is comparatively transparent. The reflected wing is large and triangular, although much shorter (transversely) than in *Oligyra*. The marginals are practically the same shape as those of *O. orbiculata*. All are evenly ligulate, with a decided tendency for the cusps to be arranged on the outside of the tips.

The radula of *H. japonica* is not figured as it is practically identical with that of *H. occulta*. One more cusp on the B-central was noted in one radula of *H. japonica* but it was absent in the other radula examined. This species also showed a slight tendency to increase the number of cusps on the marginals more rapidly than did *H. occulta* (see Table II). This practical identity of the radulae, despite the divergence in opercula, is the reason for the inclusion of *Waldemaria* as a section in the genus *Hendersonia*. I am very doubtful if *Miluna* even deserves sectional rank, but have seen no specimens.

TABLE II. RADULAR FORMULAE IN *Hendersonia* AND *Oligyra*.

	Centrals			Comb	Marginals						Grand
	A	B	C	Lateral	2	3	4	5	6	Total	Total.
H. occulta	5	5	4	6		7	5	5	5	39–40	89–91
H. japonica	5	5–6	4	6		5	7	5	5	42–43	95–97
A. verecunda	7	8	4	10–11		1*	2+3	4	3	50	111
O. orbiculata	4	6	4	6		3	4	10	7	52	115
O. convexa	4	6	4	7	1*	2+3	2	2	4	81	173
O. f. strebeli	5	8–9	4	7		3	4	3	3	58–62	127–134
O. o. coccinostoma	4	7	4	7		5	3	3	3	90	191
O. cacaguelita	2?	4	4	7		4	6	2	4	95	201
O. riparia	5	5	4	9–10		7	6	5		73	157
O. rotunda	4	5	4	7	1	10	7			82	175
O. palliata	5	5	4	8		10	5	4	5	123	257

The radula of *Hendersonia* is very close to that of *Oligyra*, and the separation of the two, on this basis alone, might be rather difficult. However, the shell-characters of *Hendersonia*, its wide distribution, and its significance as a primitive, holarctic group

certainly demands it generic recognition. It seems that *Hendersonia* is a primitive genus which once had a wide holarctic distribution, but which only survives in a few localities in Asia and North America. The case of the giant salamander amongst the amphibians (Ohio River, U. S.; and Japan) appears to be analogous. In this connection the genus *Dawsonella* Bradley (1872), from the Carboniferous of Indiana, is at least interesting. If it actually belongs in the Helicinidae, the circular aperture would seem to indicate that it probably possessed a spiral operculum.

An additional reason for the position of *Hendersonia* as a primitive group, was found in the study of the radula of *Aphanoconia* (*Sphaeroconia*) *verecunda* (Gould)[3]. This radula (Plate V, fig. 23) is also quite close to that of *Hendersonia*, but its divergence is along different lines from that of *Oligyra*, and apparently denotes a divergent line of evolution. The large number of cusps on the peculiar paired centrals (Table II), the long comb-laterals with numerous pointed cusps, the exceptionally long accessory plates with somewhat reduced wings, and the very long and slender marginals give an assemblage of characters that separate this group from any American one that I have examined. *H. verecunda* Gould (1859) is here chosen as the type of *Sphaeroconia* A. J. Wagner (1909). *Verecunda* A. J. W. (1909) is an exact synonym.

Pilsbry and Cooke (1908) have described the radulae of *H. baldwini*, *uberta*, *laciniosa*, and *rotelloidea* from Hawaii, and figured those first and third. From their studies, it appears that the radula of *Sturanya* Wagner (1905) (Type *H. laciniosa* Mighels, 1845) is very close to that of *Sphaeroconia*, but that the radula of *Orobophana* Wagner, 1905 (type *H. uberta* Gould, 1847), as they point out, is considerably different.

Genus **OLIGYRA** Say. Tropical and Subtropical America.
Subgenus OLIGYRA s. s. Same distribution.
Section OLIGYRA s. s. United States; New Mexico, Bermudas etc.

Olygyra Say (1818). Type (monotype) *O. orbiculata* Say (1818). Eastern Fla., U. S.
Oligyra Say (1819). Emended form of preceding; emended by Say himself.
Orbiculata A. J. Wagner (1905). Type (by tautonomy) *O. orbiculata* Say (1818).

[3] 1 dried specimen; A. N. S. P. no. 78852; collected at Ryukyu, by Y. Hirase (1900).

? *Subglobulosa* A. J. W. (1905).[4] Type (by tautonomy) *H. subglobulosa* Poey (1852). Cuba.

O. orbiculata orbiculata Say (1818). Mouth St. Johns R., Fla. (s. U. S.).

?? *H. ambeliana* Sowerby (1842).

?? *H. vestita* "Guild." Sowerby (1842). N. A. Young shell; might be any helicinid.

H. hanleyana Pfr. (1849). New Orleans, La., U. S.

H. suborbiculta and *H. subtropica* appear to be Ms. names.

O. orbiculata tropica ("Jan" Pfr.) (1850).Tampico, Mex. (and s. w. U. S.).

O. orbiculata clappi (Pilsbry) (1909). Central and Eastern Fla.

?**O. borealis** (von Martens) (1890). Villa Lerdo, Durango, Mex.

??**O. cordillerae** ("Salle"Pfr.) (1857). 3500 meters, Mt. Orizaba, V. C. Mex.

O. convexa (Pfr.) (1849). Bermuda Islands.

In this typical section, the radula of the type species,[5] and that of *O. convexa*[6] have been examined. The radular formulae are given in Table II. The centrals of *O. orbiculata* (Plate III, fig. 2) are similar to those of *Hendersonia*, but the R-central has a less attenuate base, and the C-central has considerably smaller cusps. The comb-lateral is somewhat lighter, while the accessory plate is both lighter and much more elongate transversely (Plate IV, fig. 11). The wing is somewhat reduced, and gives a lanceolate outline. The marginals are very close to those of *Hendersonia*, but are slightly more numerous.

The radula of *O. convexa* is not figured, but it is very close to that of *O. orbiculata*. The formula is given in Table II. The shell of *O. convexa* is also very similar to that of *O. orbiculata*; it is of the same depressed form and has a similarly thickened peristome. In this connection, a number of Antillean species, included by A. J. Wagner in the sections *Subglobulosa* and *Festiva*, need examination. Many of them have the calcareous, light-colored opercula of this group.

This group has many primitive characters, but in the reduction of the wing on the accessory plate, slightly approaches *Oxyrhombus* of *Helicina*. Its closest relatives are in the section *Succincta*, thru which it is connected with *Alcadia*. As indicated in the relationship diagram in Table I, it probably represents a primitive stock near the ancestral line of the genus *Helicina*. The distribution of the species appears to sustain this idea. If the Antillean species

[4] Groups preceded by a question-mark are those of which I have not examined the radula; species preceded by a question-mark are those I have not seen; in the latter, 2 question-marks indicate considerable doubt as to its position or specific rank.

[5] 5 alcoholic specimens; A. N. S. P. no. 91705; collected near Frierson, La., by L. S. Frierson (1906).

[6] 2 alcoholic specimens; A. N. S. P. no. 85558; collected on flats near Frascati Hotel, Bermuda, by A. Gulick (1903).

actually belong here, this section will be represented around the main West Indian centers of evolution, but is best represented in places where it does not come into competition with the more advanced types of the Helicinidae.

Section SUCCINCTA A. J. Wagner. Mex. to S. A.

Succincta A. J. W. (1905). Type (by tautonomy) *H. succincta* von Martens (1890). Mexico.

Gemma A. J. W. (1907). Type (by tautonomy) *H. gemma* Preston (1903). Costa Rica. Not *Gemma* Deshayes (1853) teste Fischer (1885).

O. arenicola (Morelet) (1849). Sisal, Yucatan.

O. arenicola raresulcata (Pfr.) (1861). Vera Cruz, Mex., sandy.

O. arenicola succincta (von Martens) (1890). Cordova, V. C., Mex.

O. flavida flavida (Menke) (1828). Described as from Jamacia, but not since found there. Generally recognized as Guat.

??? *H. ambieliana* Boissy (1835). Tobago, Antilles; more probably near *H. fasciata* Lam.

H. trossula Morelet (1849). Vera Paz, Guatemala.

?**O. flavida brevilabris** (Pfr.) (1857). Guatemala. A larger form.

? *H. microdina incommoda* A. J. W. (1905). Guatemala.

O. flavida strebeli (Pfr.) (1861). Mirador, Vera Cruz, Mex.

O. oaxacana (Pilsbry) (1920). Puerto Angel, Oaxaca, Mex.

? *H. microdina* A. J. W. (1905, 1910), not Morelet (1851). Vera Paz, Guat.

O. fragilis fragilis (Morelet) (1851). Peten, Guatemala.

O. fragilis elata (Shuttleworth) (1852). Cordova, Vera Cruz, Mex.

O. fragilis merdigera ("Sallé" Pfr.) (1855). Vera Cruz, V. C., Mex.

? *H. mohriana* Pfr. (1861). Orizaba, Vera Cruz, Mex. (intermediate between two).

O. oweniana oweniana (Pfr.) (1849). Chiapas, Mex.

O. oweniana coccinostoma (Morelets) (1849). Vera Paz, Guat. (very close).

? *H. anozona* von Martens (1875). Coban, Guat. (color form).

O. beatrix beatrix (Angas) (1879). Costa Rica.

?**O. beatrix nicaraguae** (A. J. W.) (1908). Nicaragua.

??**O. beatrix confusa** (A. J. W.) (1908). Costa Rica. (figure looks more like next).

O. gemma (Preston) (1903). Costa Rica[7].

In this section, the radulae of *O. flavida strebeli*[8], *O. oweniana coccinostoma*[9], and a form near *O. cacaguelita* (Pilsbry and Clapp) (1903)[10] have been examined. The radular formulae of all three forms are shown in Table II, while the first two species are figured. The radula of *O. flavida strebeli* (Plate III, fig. 3; Plate IV, fig. 12) is very similar to that of *Oligyra* s. s., but shows a divergence in the

[7] *H. antoni* Pfr. (1848) was described originally without habitat; in Chemnitz it is figured with the habitat Sandwich and Gambier I. (South Pacific); while in 1852, the habitat is given as Honduras. From the figure and description, I doubt if it is an American shell, but consider it near *H. pazi* "Hidalgo" Crosse (1865), also from the same general region as the habitat given in the second paper.

[8] 1 alcoholic and 5 dried specimens; collected on U. of Mich.-Walker Exped. in Vera Cruz Mex.; Hacienda Cuatotolapam, Canton Acayucan (1910)

[9] 1 dried specimen; A. N. S. P. no. 107628, collected in mts. w. of Livingston, in Guat. by A. A. Hinkley (1913).

[10] 2 dried specimens; A. N. S. P. no. 146582; collected at Cincinnati, Sierra Santa Marta Colombia, by Rehn and Hebard. (1920).

better development of the wing on the accessory plate, which is more like that of the subgenus *Alcadia*. The centrals are closer to those of *Oligyra* s. s., as is also the comb-lateral. As shown in the synoptic key, the especial characteristics of this group are: the wing on the marginals, the increased number of teeth, and the tendency for the cusps on the A-central to be reduced to a small number at the extreme outer tip. This last character and the wing on the marginals, which is shown in the figure of *O. oweniana coccinostoma* (Plate V, fig. 24), separate *Succincta* from all other groups. In *O. cacaguelita*, the A-central has a triangular expansion of the tip, similar to the other species, but the cusps are either practically absent or are very much worn in the species, as compared to *O. f. strebeli*, is probably correlated with the difference in size. All of the species show a tendency to increase the number of the cusps on the marginals very rapidly.

O. cacaguelita is the only South American species that I can place definitely in this group. The section *Tamsiana*, which Wagner places very near his section *Gemma*, appears from the radula, and also from the texture of the operculum, to be a section in *Helicina*.

Subgenus ALCADIA Gray. West Indies to So. America.

Alcadia Gray (1840). Type *H. major* Gray (1825). Jamaica.
Eucaladia, Eualcadia A. J. W. (1907). Type (used as *Alcadia* s. s.) *H. major* Gray.
Palliata A. J. Wagner (1907). Type (by tautonomy) *H. palliata* C. B. Adams (1849). Jamaica.
?Hispida A. J. W. (1907). Type (by tautonomy) *H. hispida* Pfr. (1839). Cuba.[11]
? Intusplicata A. J. W. (1907). Type (by tautonomy) *H. intusplicata* Pfr. (1850). Haiti.
Incrustata A. W. (1907). Type (by tautonomy) *H. incrustata* "Gund." Pfr. (1859). Cuba.
Sericea A. J. W. (1907). Type (by tautonomy) *H. sericea* Drouet (1859). Cayenne.

Section IDESA H. and A. Adams. West Indies.

Idesa H. and A. Adams (1856). Type (Fischer[12]) *H. rotunda* d. Orbigny (1845). Cuba.

[11] The last three sectional names are included simply for completeness; they may represent perfectly valid groups.

[12] Fischer (1885) names the type of the genus *Helicina*, and then gives, in parentheses and without remark, examples of each group. However, he seems to make an attempt to name the types, as in the first group they are correctly given. For this reason, I have chosen, as far as possible, his examples as types of each group. *Emoda* H. and A. Adams is an exception, as A. J. Wagner, contrary to his usual habit, uses this group in an emended sense.

Leialcadia A. J. Wagner (1907). Type (now chosen, as used by author as *Idesa*) *H. rotunda* d. Orbigny (1845).

Nitida A. J. W. (1907). Type (by tautonomy) *H. nitida* Pfr. (1839). Cuba.

Megastoma A. J. W. (1907). Type (by tautonomy) *H. megastoma* C. B. Adams (1849) Jamaica. Not *Megastoma* Morris and Lycett (1850), Costa (1850), nor Swainson (1837).

Mamilla A. J. Wagner (1907). Type (by tautonomy) *A. mammilla* Weinland (1862) (*A. mamilla* A. J. W.). Not *Mamilla* Tryson (1883), emendation of *Mammilla* Schumacher (1817).

? Bellula A. J. Wagner (1907). Type *H. bellula* "Gund." Pfr. (1859) Cuba.

? Ampliata A. J. Wagner(1907). Type *H. ampliata* C. B. Adams (1850). Jamaica.[13]

Section ANALCADIA A. J. W. Antilles to Central America.

Analcadia A. J. W. (1907). Type (now chosen) *H. dysoni* Pfr. (1849). Cumana, Venezuela.

?**O. dysoni bocourti** (C. and F.) (1869). Belize, Honduras.

??**O. dysoni diaphana** (Pfr.) (1851). Honduras (small, angulate form).

?H. dysoni jasoni von Martens (1890). Isle Bonacca, Honduras.

???**O. sanguinea** (Pfr.) (1849). Honduras (Dyson). Probably an Antillean species.

In this subgenus the radulae of *C. palliata*[14], *O. rotunda*[15], and *O. riparia* (Pfr.)[16] were examined. All are included in Table II, but only *O. palliata* is figured (Plate V, fig. 25) here. The differences are indicated in the synoptic key, and in Table II. Except for the broad R-central of *O. dysoni*, they differ mainly in size.

From the indications given by these few radulae, *Alcadia* appears very close to *Oligyra* s. s. A. J. Wagner (1907) has shown in his study of the opercula and shell characters, that the Mexican species, which he groups around *O. gemma*, are connected, in these particulars, by an intergrading series with the typical forms of *Alcadia*. In the radulae, the biggest break comes between the West Indian forms and those of the mainland (exclusive of *Analcadia*). Nevertheless, the whole group of radulae, included here in the genus *Oligyra*, form a very closely related group, separated from other genera by quite distinctive characters. It is true that the subgenus *Alcadia* and the subgenus *Oligyra* appear to represent the basal members of two diverging lines of evolution, but at present it would be extremely difficult to name any very definite characters for their separation.

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[13] The last two sectional names can be used.

[14] 2 dried specimens; A. N. S. P. no. 101204; collected at Somerset, Manchester, Jamaica by A. P. Brown (1910).

[15] 1 dried specimen; A. N. S. P. no. 77022; collected at Marianao, near Havana, Cuba, by S. N. Rhoads (1899).

[16] 2 alcoholic specimens; collected for Univ. of Mich. Museum, near La Fria, Estado Tachira, Venezuela (1920).

Genus **HELICINA** Lamarck. Tropical America.

Subgenus TRISTRAMIA Crosse. Mainland.

Section OXYRHOMBUS C. and E. Mexico to South America.

Oxyrhombus Crosse and Fisher (1893). Type (now chosen) *H. amoena* (1849). Honduras.
Concentrica A. J. W. (1905). Type (by tautonomy)*H. concentrica* Pfr. (1849). Merida, Venezula.
Punctisalcata A. J. W. (1905). Type (by tautonomy) *H. punctisulcata* von Martens (1890).
Punctisulcata A. J. W. (1910). Corrected form of preceding.
Cinctella A. J. W. (1910). Type (by tautonomy) *H. cinctella* Sh. (1852). Mexico. Not *Cinctella* Monterosato (1884).

H. cinctella cinctella Shuttleworth (1852). Orizaba, Mex.
H. botteriana Pfr. (1856). Orizaba, Mexico.
?H. cinctella bautistae A. J. W. (1910). Tabasco, Mex.
?H. punctisulcata punctisulcata von Martens (1890). Omiltem, Guerrero, 8000 ft.
H. punctisalcata A. J. W. (1905).
??H. punctisulcata zunilensis A. J. W. (1910). Zunil, Guatemala.
H. amoena Pfr. (1849). Honduras. (Mex. to Panama).
H. purpureoflava Morelet (1849). Guatemala.
H. sowerbyana Pfr. (1849). Guatemala??? Victoria, Tamaulipas, Mex. (Pilsbry).
H. ghiesbreghti Pfr. (1857). Chiapas, Mexico.
H. ghisbrechti, ghisbrecti, ghiesbrechti, ghisbreghti, auct.
??? *H. sinuosa* Sowerby (1866) and A. J. Wagner (1910)[17].

In this group, the radulae of *H. amoena*[18], *H. cinctella*[19], and *H. concentrica*,[20] have been examined. The radular formulae of all three species is given in Table III, while that of *H. amoena* is figured (Plate III, fig. 8; Plate IV, 15). Especially noteworthy are the well-developed, sharp-pointed cusps on the A and C centrals, and the numerous pointed cusps on the comb-lateral. The narrowly reflected border of the accessory plate simply joins the outer continuation of the cusp-bearing portion of the comb-lateral. The "handle" of the comb-lateral had a peculiar lamellar thickening where it crosses obliquely the basal, spoon-shaped portion on the tooth. On superficial examination, this might easily be mistaken for a wing to the accessory plate.

Although there is considerable break between the radula of this group and that of *Oligyra* s. s., the operculum shows intergrading characters. The horny portion is *Helicina*-like in *Oxyrhombus*, but the calcareous portion is usually somewhat thickened, especially

[17] As pointed out by von Martens (1890), this is certainly not *H. sinuosa* Pfr. (1850). Wagner got his specimens from Sowerby and Fulton.
[18] 2 dried specimens; A. N. S. P. no. 114828; collected at Gualan, Guatemala, by S. N. Rhoads.
[19] 2 dried specimens; A. N. S. P. no. 14577; collected in Mexico, by Sallé (labeled *botteriana*).
[20] 2 alcoholic specimens; collected for Univ. of Mich. Museum, near La Fria, Estado Tachira, Venezuela.

over the nucleus; this thickening is peculiarly dead-white to bluish. Probably most of the rather elevated, carinate or subcarinate species of *Helicina* of the Andes belong here. I hope to treat them more fully in a future paper, as I have a number of specimens from the foot-hills of the Andes, near the Venezuela-Colombian border.

Section TAMSIANA A. J. W. Northern South America.

Tamsiana A. J. W. (1907). Type (by tautonomy) *H. tamsiana* Pfr. (1850). Venezuela.

In this section, the radulae of *H. tamsiana appuni* von Martens (1873)[21] and *H. nemoralis* Guppy (1866)[22] have been examined. I expect to describe them more fully in a future paper, as I have numerous specimens of this group, from various localities in the Cumbres Mts., Venezuela. The radular formulae are shown in Table III.

Although nearest *Oxyrhombus*, both in shell and radular characters, this group shows certain resemblances to *Helicina* s. s., on account of the more rounded cusps on the comb-lateral and the rather peculiar development of the A-central. The marginals are strictly ligulate. The operculum is similar to that of *Oxyrhombus* in texture, but *H. sanctaemarthae* Pilsbry and Clapp (1902), which probably belongs here, has the best development of the calcareous plate that I have seen in any true *Helicina*.

Section ANGULATA A. J. W. 1905. South America to Central America.

Angulata A. J. W. (1905). Type (by tautonomy) *H. angulata* Sowerby (1842). Brazil.

Variabilis A. J. W. (1905). Type (by tautonomy) *H. variabilis* Wagner (1827). Brazil.

? H. candeana "d'Orbigny" Sowerby (1842). Bay of Honduras.[23]

?H. oxyrhyncha Crosse and Debeaux (1863). Habitat ??. A little larger shell..

?H. oxyrhinca of authors.

??H. rhynchostoma from Central America, of authors.

?H. pterophora Sykes (1902). Guatemala[24].

?H. oxyrhyncha Wagner (1910). Isle of Bonacca, Bay of Honduras[25].

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[21] 2 alcoholic specimens; collected for Univ. of Mich. Museum, near Palma Sola, Estado Falcon, Venezuela (1920).

[22] 1 dried specimen; A. N. S. P. no. 14610; collected (by Guppy?) in Island of Trinadad.

[23] Not in d'Orbigny (1835 or 1837). As Sowerby says this shell is smooth, it cannot be *candeana* of authors, from Venezuela (Cf. *H. rhynchostoma ernesti* von Martens (1873), as that form has very evident spiral striations.

[24] Ancey (1904) says this is identical with *oxyrhyncha*; the figures and description certainly coincide very well with *candeana*.

[25] There may be a mainland and an insular subspecies, but they are not separable from the descriptions or figures.

In this group, the radulae of *H. caracolla* Moricand (1836)[26] and that of *H. rhynchostoma ernesti* von Martens[27] have been examined. The formulae are given in Table III, and I expect to study the group more thoroughly in the near future, as I have many specimens from the Cumbres Mts., and Aroa Valley, Venezuela.

The radula of this group like the shell-characters, are more or less transitional between *Oxyrhombus* and *Tristramia* s. s. The A-central has a heavy cutting edge, which is without cusps in the specimen of *ernesti* examined, but usually bears one or two heavy, irregular points in *caracolla*. The C-central has two large, rounded, hook-like points and in *caracolla* has one or two minor points in addition. The single Central American species appears closest to *H. rhynchostoma* "Sh." Pfr. (1865), but also resembles considerably *H. rostrata* Morelet, as pointed out by Crosse (1863).

Section TENUIS A. J. W. Mexico to Central America; South America.

Tenuis A. J. W. (1910). Type (by tautonomy) *H. tenuis* Pfr. (1849). Mexico.

H. tenuis tenuis Pfeiffer (1849). Yucatan, Mexico.
H. vernalis Mo. (1849). Peten, Guatemala.
H. lindeni Pfr. (1849). Tapinapa, Mexico.
H. chiapensis Pfr. (1856). Chiapa, Chiapas, Mexico.
H. lindeni minor Ancey (1886) Honduras.
H. lindeni verapazensis A. J. W. (1905). Vera Paz, Guatemala.
?**H. tenuis pittieri** A. J. W. (1910). Rio de los Plutunales, Golfe Dolce, Costa Rica.
??**H. senachuensis** A. J. W. (1910). Senachu, Guatemala.
H. delicatula delicatula Sh. (1852). Cordova, Mex.
H. heloisae "Salle" Pfr. (1856). Cordova, Mexico.
H. delicatula notata "Sallé" Pfr. (1856). Cordova, Mex.
?**H. durangoana durangoana** Mousson (1883). Durango, Mex.
?**H. durangoana sagulensis** A. J. W. (1910). Jalisco, Mex.

The radula of the type species[23] was examined, and the radular formula is given in Table III. It differs from that of *H. zephyrina* by the presence of 4 small cusplets on the C-central, but agrees with it in the lack of cusps and the development of the thickened cutting edge of the A-central (Plate III, fig. 7; Plate IV fig. 14). The cusps of the marginals are not arranged as completely on the tip of the tooth as in *H. zephyrina.*

Section TRISTRAMIA S. S. Mexico to Colombia.

Tristramia Crosse (1863). Type (monotype) *H. salvini* Tristram (1861). Guatemala.

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[26] 2 dried specimens A. N. S. P. no. 14622; collected in Brazil, by J. C. Anthony.
[27] 1 alcoholic specimen; collected for the Univ. of Mich. Museum, at Palma Sola, Estado Falcon, Venezuela (1920).
[28] 4 specimens; University of Mich.-Walker Expedition to Southern Vera Cruz, Mexico; Hacienda Cuatotolapam, Canton Acayucan.

Caloplisma C. and F. (1893). Type (monotype) *H. rostrata* Morelet (1851). Guatemala.
Retorquata A. J. W. (1905). Type (first species) *H. zephyrina* Duclos (1833). Mexico.
Turbinata A. J. W. (1905). Type (by tautonomy) *H. turbinata* "Wieg. Menke" Pfr. (1846). Mexico.
Rostrata A. J. W. (1905). Type (by tautonomy) *H. rostrata* Mo. (1851). Not *Rostrata* Gray (1855).

H. rostrata rostrata Morelet (1851). Vera Paz, Guatemala.
H. salvini Tristram (1861). Coban, Guatemala.
H. rostrata simplex C. and F. (1893).
H. dalli "Bartsch" Fluck (1906). Wani, Nicaragua (bare name).
?**H. rostrata mategalpensis** A. J. W. (1910). Matagalpa, Nicaragua.
H. rostrata denticulata Pfr. (1855). Honduras.
H. funcki funcki Pfr. (1849). S. Yago, New Granada.
H. funcki costaricensis A. J. W. (1905). San Jose and Santa Clara, Costa Rica.
?**H. funcki pitalensis** A. J. W. (1910). El Pital, Rio Naranjo, s. w. Costa Rica.
H. funcki parvidens Pilsbry (1920). Juen Vinas, 3000-3300 ft., Costa Rica.
H. zephyrina zephyrina Duclos (1833). Tampico to Nicaragua.
H. turbinata "Wieg. Menke" Pfr. (1848).
?? *H. ambeliana* Sowerby (1842).
? *H. sinuosa* Pfr. (1850). Mexico? Monstrosity?
? *H. sandozi* Sh. (1852). Monstrosity.
H. berendti Pfr. (1861). Vera Cruz, Mex. Excavatoangulate var. of Mart. (1908).
H. turbinata minima Strebel (1873). Not *H. minima* d'Orb. (1845).
H. zephyrina elatior "von Marten" C. and F. (1893)=higher race.
??**H. zephyrina deppeana** von Martens (1863). Oaxaca, Mex.
H. zephyrina dientensis Pilsbry (1903). Diente, Nuevo Leon, Mex.
H. chrysocheila chrysocheila A. Binney (1851). s. w. U. S (Tex. to N. Mex.).
H. chrysocheila shuttleworthi von Martens (1890). Cordova, V. C., Mex.
H. chrysocheila Sh. (1852), not Binney (1851).
H. chrysocheila vanattae Pilsbry (1909). Los Canoas, San Luis Potosi, Mex.

In this group, the radula of *H. zephyrina*[29] was examined. The radular formula is given in Table III. No cusps are present on the A-central (Plate III, fig. 9); the B-central is simply a curved, almost rectangular plate with spatulate crenulations on the upper margin. The lanceolate C-central bears one, large, rounded hook. The comb-lateral (Plate IV, fig. 13) is heavy and bears large, spatulate cusps. The accessory plate is small and has but little reflection of the anterior border. The marginals are large and quite strictly ligulate; the bases form oblique rows but the tips are in nearly transverse rows, at least towards the center. The cusps of each tip form disc-like crowns, with the cusps arranged transversely on each. The calcareous operculum is degenerate, but the horny operculum is thick and brilliantly colored red. This group, to my mind, represents the most complete development of the genus *Helicina* on the mainland.

[29] 3 alcoholic specimens; University of Michigan-Walker Expedition in Southern Vera Cruz, Mexico; Hacienda Cuatotolapam, Canton Acayucan (1910).

Subgenus HELICINA s. s. West Indies.

Helicina Lamarack (1799, 1801). Type *H. neritella* Lam. (1799). Jamaica.
Pitonnellus, Pitonnillus Montfort (1810). Type *H. neritella* Lam. (*Pitonillus* auct.).
? *Pachytoma* Swainson (1840). Type *H. occidentalis* Guilding (1828). Saint Vincent I.
Pachystoma auct., not *Pachystoma* Guilding (1828).
Euneritella A. J. W. (1905). Type (by tautonomy) *H. neritella* Lam.
?? *Subglobulosa* A. J. W. (1905). Type (by tautonomy) *H. subglobulosa* Poey (1852) Cuba.
?? *Festiva* A. J. W. (1910). Type (by tautonomy) *H. festiva* Sowerby (1839) Haiti. Not *Festivus* Crotch (1872) nor *Festiva* Gray (group larger than genus).

I have been able to obtain but one specimen of *H. neritella diplocheila* A. J. W.[30] The animal was almost completely destroyed by dermestids, but by washing it out carefully, I obtained examples of all of the kinds of teeth, and a few clumps with the centrals, comb-laterals, accessory plate, and a few of the inner marginals still clinging together. The centrals are not arranged in their natural position in the figure (Plate III, fig. 6), and the R-central, especially is not foreshortened as usually seen.

The markings of the R-central are peculiar. The A-central has a peculiar shelf-like projection, which bears three, deep-set, large, rounded cusps. The B and C centrals are very similar to those of *Tenuis*, but are shown from a somewhat different angle. The comb-lateral has a rather narrow basal plate (Plate IV, fig. 17). The accessory plate has a small body but a large lanceolate appendix, and the reflected anterior portion forms a quite prominent shelf, which juts out almost at right angles to the body of the plate. The innermost marginals are very short and broad, not over one-half as long as the longest ones. All of the definitive marginals have sickle-shaped tips, with wings which remotely resemble those of the section *Succincta* of *Oligyra*, but are much better-developed.

In addition, I have examined *H. adspersa* Pfr. (1839), both the large, typical form and a smaller variety *H. a. marmorata* d'Orb. (1845)=*H. tenuilabris* Pfr. (1848)[31]. This Cuban species has sharper cusps on the A-central (Plate VII, fig. 37) and also on the comb-lateral (Plate IV, fig. 17 A). The wings on the marginals are more prominent than in *H. neritella*, and, in certain views,

[30] 1 dried specimen; A. N. S. P. no. 104391; collected at Orange Hill, Montego Bay, Jamaica, by A. P. Brown. This is *H. n. angulata* C. B. Adams (1851), not *H. angulata* Sowerby (1842).

[31] 3 alcoholic specimens, sent me by John B. Henderson; from Western Cuba.

appear to be marked off proximad by a slight groove, so that they have much the appearance of large, triangular cusps. The small form is the one figured; it has a much smaller number of the marginals (80 as against 106), and the comb-lateral has one more cusp and all are longer and narrower than in the larger form. This species is apparently quite closely related to *H. neritella*.

The operculum of this group is very similar to that of *Tristramia*, s. s. It has a heavy, reddish, horny plate, and a thin calcareous plate; the latter is somewhat thickened towards the columellar but incomplete towards the palatal margin. Although the group certainly belongs with *Tristramia*, it is rather divergent and needs further study before any accurate estimate of its relationship can be stated. As already remarked, there are certain resemblances to *Tamsiana*, and it is possible that the two groups connect up in the lesser Antilles. Many of the species included in *Subglobulosa* A. J. W. and *Festiva* A. J. W. have the yellowish operculum, with the poorly-developed horny plate, which is more characteristic of *Oligyra* than of this group.

TABLE III. RADULAR FORMULAE IN *Helicina*, *Lucidella*, AND *Schasicheila*.

	Centrals			Comb	Marginals.				Grand	
	A	B	C	Lateral	2	3	4	5	Total	Total
H. amoena.....	5	5	4	9–10		6	4	6	70	151
H. cinctella.....	5	6–8	4	9		4	6	5	83	177
H. concentrica.....	5	4	5	11		1*	3+4	7	79	169
H. tamsiana appuni	4	4	4	8		5	3	5	87	185
H. nemoralis.....	4	5	4	9–10		5	2	7	108	227
H. caracolla.....1–2		5	4	10		3	5	8	83	177
H. r. ernesti.....	0	6	2	9–10		2	14	5	89	189
H. tenuis.....	0	6	4	7	1*	1+8	5	5	70	151
H. zephyrina.....	0	7	1	8	2*	1+7	5	5	102	215
H. neritella.....	3	6	4	7	1*	2+6	?	?	many	many
H. adspersa.....	3	4–5	4	9	2*	3+4	5	7	106	223
S. silacea.....	4	4	4	9–104		5	6	9	78	167
S. sagraiana.....	4	4	4	9	2*	1+6	6	8	80	171
S. ciliata.....	4	4	4	6	1	8(5)*	4+9		58	127
S. hidalgoana.....	3	4	4	6	9	6	5		46	103
L. venezuelensis....	4	5	4	9		7			40	91
L. lirata.....	2	7	6	6		5	12		62	135
L. aureola.....	1	7	5	9–10	2	21	20		136	283

Genus **LUCIDELLA** Swainson. Tropical America.

?Subgenus LINDSLEYA Chitty. Jamaica to South America.?

Lindsleya Chitty (1857). Type *Stoastoma lindsleyanum* C. B. Adams (1849) Jamaica.

A number of minute, globose shells (*L. venezuelensis* n. sp.), which were collected near Palma Sola, Estado Falcon, Venezuela (1920), closely resemble this Jamaican group, which originally was described as a genus of "Stoastomidae." The margin of the aperture is entire, but quite simple, and the shell is well-perforated. The sculpture consists of well-marked spiral ridglets. The calcareous plate of the operculum is rather heavy, and is quite markedly concave externally.

On examination of the radula (1 dried specimen), I was greatly surprised to find it very close to that of *Lucidella lirata* (Plate III, fig. 5; Plate V, fig. 21), and totally unlike that of *Stoastoma* (Plate VI, fig. 26). It differs from that of *L. lirata* in the presence of several cusps on the upper margin of the hood-shaped A-central, in the lanceolate C-central without the accessory lateral cusp, and in the larger number of cusps (like *L. aureola*) on the comb-lateral. It is the smallest Helicinid radula that I have examined.

On account of the very similar shell-characters, it is placed tentatively in the subgenus *Lindsleya*, which is transferred to the genus *Lucidella*. If the shell-characters are any key to their relationship, I suspect that all of the species of this group and part of those in *Metcalfeia* belong here, as they do not possess the lip expansion and upper sinus, characteristic of true *Stoastoma*. This would restrict the latter genus to Jamaica, as *S. haitianum* Weinland and *S. domingensis* Vanatta from Haiti, and *S. portoricense* Pfr. from Porto Rico, lack these typical shell characters of *Stoastoma pisum* C. B. Adams (1849). The whole *Stoastoma*-problem needs reinvestigation, as practically none of the species have been figured, and many are impossible to identify from the descriptions.

The radula and the shell of *L. venezuelensis* n. sp. will be more completely described and figured in a future paper. The radular formula is given in Table III.

Subgenus POENIA H. and A. Adams. Tropical America.

Poenia H. and A. Adams (1856). Type (Fischer) *H. unidentata* Pfr. (1849). Guatemala.
Perenna Guppy (1867). Type *H.* (*Perenna*) *lamellosa* Guppy (1867). Isle Trinidad.

L. lirata (Pfr.). (1847). Yucatan. (Mexico to Venezuela).
H. unidentata Pfr. (1849). Honduras.
H. rusticella Morelet (1849). Carmen Island, Yucatan.
? *H. semistriata* Sowerby (1866). Boca del Toro, Chiriqui, Panama (v. Mart. 1890).

L. pilsbryi Clapp (1914). Swan Island, Bay of Honduras.

L. tantilla (Pilsbry) (1902). Florida, U. S. (Cuba, Ramsden).

The radula of *L. lirata*[32] is figured (Plate III, fig. 5; Plate V, fig. 21 21), and the formula is given in Table III. The A-lateral is hood-shaped, with the opening inwards; its shape is perhaps better shown in the tilted A-lateral shown beneath the row of teeth of *Lucidella aureola* (Plate III, fig. 4). This "hood" ends distad with a curved hook, while there is also a stout point on the outer margin. It bears no true cusps. The B-central has a cuspless space on the outer tip, which fits over the C-central. The last is very long and slender, and bears a small cusp on the outer margin, besides the 4 terminal ones. The comb-lateral has a peculiar saddle-shaped expansion of the cusp-bearing border. The accessory plate is long, but very thin and transparent; it just touches the outer end of the comb-lateral. This gives the radula a peculiar appearance, as the comb-lateral appears to be set off from the inner ends of the marginals by a transparent border. The entire radula is so small as to require an oil-immersion lens for its thorough examination. Its total width is less than that of a single T-lateral of *Viana regina*.

Subgenus LUCIDELLA s. s. Jamaica; Haiti? Cuba?

Lucidella Swainson (1840). Type *Helix aureola* Ferussac (1822). Jamaica.
? *Prosopis* Weinland (1862). Type (monotype) *P. sulcata* Weinland (1862). Haiti.[33] Not *Prosopis* Fabricius (1804).

The radula of the type species [34] has been examined. It is figured from an example that had two A-centrals (Plate III, fig. 4; Plate V, fig. 22); the inner one corresponds more to the type found in the other two, normal radulae. Below the row of centrals in the normal position, a single inner A-central is shown in a slightly tilted position, so as to give a better idea of the shape. This radula differs from that of *L. lirata* mainly by the absence of the upper point on the A-central, by the broader C-central, with especially well-marked cusps, and by the greater number of cusps on the comb-lateral. The marginals are more numerous than in any other species of Helicinidae examined.

Genus **SCHASICHEILA** Sh. Mexico; western Cuba; Bahamas?

Subgenus EMODA H. and A. Adams. Western Cuba.

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[32] 2 dried specimens; A. N. S. P. no. 72171; collected in Garden of Juarez Institute, San Juan Bautista, Tabasco, Mex., by J. N. Rovirosa.

[33] This group may be valid, but its name is certainly not.

[34] 3 alcoholic specimens; A. N. S. P. no. 104533; collected in Jamaica, by A. P. Brown.

Emoda H. and A. Adams. Type (now chosen) *H. silacea* Morelet (1849). Cuba.[35]

In this group the radulae of the type species[36], *S. sagraiana* (d. Orbigny) (1845)[37], and *S. ciliata* (Poey) (1852)[38] were examined. The radular formulae of all three are included in Table III, but only the first is figured (Plate IV, fig. 16; Plate V, fig. 19).

The centrals are *Alcadia*-like as are those of *Schasicheila* s. s. The A-central has a peculiar outer plate, which fits under the C-central. The accessory plate is comparatively smaller than in any of the preceding groups, but is heavy and has a strong lobe for clasping the end of the comb-lateral. The latter is large and heavy, with spatulate cusps, and a heavy, squarish base. There are fewer cusps (6) in *S. ciliata* than in the other two species. The inner marginals are bicuspid. In *sagraiana* and *silacea*, the inner 4 or 5 have only two functional cusps, while in *ciliata* from 6 to 7 are functionally bicuspid. The difference between this statement and the formulae, as given in Table III, is due to a small vestigial tooth that appears quite variable in its occurrence. The marginals are peculiarly heavy and wooden, like those of *Schasichelia* s. s., and are not very numerous for such large shells. *S. ciliata* has a smaller number of marginals than the other two.

The shells of this group are amongst the largest and heaviest of the entire family. In external appearance, they resemble those of *Analcadia*, but the radula is distinctly *Schasicheila*-like, as is also the sculpture of such species as *S. ciliata*. The latter probably belongs in a different section than do the other two species. The close relationship between *Emoda* and *Schasicheila* s. s. presents additional evidence for the former land connection between Cuba and Yucatan.

Subgenus SCHASICHEILA s. s. Mexico, Guatemala.

Schasicheila Shuttleworth (1852). Type (Fischer) *S. nicoleti* Sh. (1852). Mexico.
Schasichila and *Schazicheila* auct.

S. alata ("Menke"Pfr.). (1848). Cordova, Mexico.
S. pannucea Sowerby (1866), non Morelet.

S. fragilis Pilsbry (1899). Diente, Nuevo Leon, Mexico.

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[35] As this group is used by Wagner (1907) in an emended sense, it was thought best to choose a type from those of the species of H. and A. Adams, which are also included by Wagner.

[36] 2 alcoholic specimens; A. N. S. P. no. 110833; collected at Tabajo, Yunquede, Baracoa, Cuba. by Chas. T. Ramsden.

[37] 3 alcoholic specimens; sent me by John B. Henderson; from western Cuba.

[38] 1 mounted slide from the collection of A. N. S. P.; made by A. P. Brown.

S. hidalgoana Dall (1897). Encarnacion, Hidalgo, Mex.; near Victoria, Tam., Mex.
S. hinkleyi Pilsbry (1919). Chama, Guatemala.
???**S. minima** "Pfr." Strebel (1873). Figure only, unindentifiable.
S. minuscula (Pfr.) (1859). Mexico.
S. miniuscula auct.
S. nicoleti Shuttleworth (1852). Cordova, Mexico.
S. palmeri Dall (1905). Alvarez Mts., San Luis Potosi; Omealca, V. C., Mex.
S. pannucea (Morelet) (1849). Peten, Guatemala.
H. alata Adams (1856), not Pfr.
?**S. pannucea misantlensis** Strebel (1873). Misantla, V. C., Mex.
?**S. pilsbryi** A. J. Wagner (1910). Mexico, Guatemala.
S. vanattai Pilsbry (1899). Diente, Nuevo Leon, Mexico.
S. vanattai tricostata Pilsbry (1903). Near Victoria, Tamaulipas, Mex.
S. xanthia Pilsbry (1909). Los Canoas, San Luis Potosi, Mex.

The radula of *S. hidalgoana*[39] is figured (Plate V, figs. 18 and 20). The centrals are somewhat *Alcadia*-like; the B-central has an outer projection that fits under the C-central. The comb-lateral is large and heavy and has a squarish base, but the outer triangular projection is so thin and weak as to be difficult to see. The accessory plate is rather small and not very heavy. The inner 9 marginals are bicuspid and resemble those of *Emoda*, although the blades are considerably longer and more close-ranked than in that group. The small number (46) is striking in a shell as large as the present species.

The distinctive shell characters were noted early, and are so peculiar as to probably warrant the generic separation of this group and *Emoda*, but the writer did not wish to erect the latter into a genus until a more thorough study of the West Indian forms had been made. The species from the mainland of North America, given above, constitute simply an alphabetic list of the names that have been proposed.

Genus **STOASTOMA** Adams. Jamaica.

Stoastoma C. B. Adams (1849). Type *S. pisum* C. B. Adams (1849). Jamaica.
Hemicyclostoma "C. B. Adams" Pfr. (1865). Type *S. pisum*.
? *Lewisia* Chitty (1857). Type *S. philippianum* C. B. Adams (1850).
? *Wilkinsonia* Chitty (1857) Type *S. wilkinsoniae* C. B. Adams (1849).
? *Fadyenia* Chitty (1857). Type *S. fadyenianum* C. B. Adams (1849).
? *Metcalfeia* Chitty (1857). Type *S. chittyanum* C. B. Adams (1849).
? *Petitia* Chitty (1857). Type *S. petitianum* C. B. Adams (1849).
?? *Lindsleya* Chitty (1857). Type *S. lindsleyanum* C. B. Adams (1849).[40]
? *Blandia* Chitty (1857). Type *S. blandianum* C. B. Adams (1849).

The radula of the type species has already been figured by Pilsbry

[39] 2 dried specimens; A. N. S. P. no. 85919; collected in canon 4 miles west of Victoria, Tamaulipas, Mexico, by S. N. Rhoads (1903).
[40] The second name in this list is an exact synonym of *Stoastoma*; the remainder may be distinct. I have already tentatively included *Lindsleya* under *Lucidella*.

(1910), and that of another specimen[41] is given here (Plate VI, fig. 26). As Pilsbry has already pointed out, this radula is truly helicinid in character. Although possessing certain marked, individual peculiarities, in others it forms a connecting link between the Vianinae and the Helicininae.

The A-central is heavy and has a single, large, outer hook which makes it superficially resemble that of *Lucidella*. The, B-central has three heavy cusps and somewhat resembles that of the more primitive species of *Eutrochatella*. The comb-lateral has only 3 large cusps, and the heavy outer process is more like that of the Vianinae than like any of the preceding genera. Nevertheless, in general shape it is distinct, and more closely related to the Helicininae. The accessory plate is small and heavy and has an inner projection which fits behind the outer end of the comb-lateral. The anterior edge is slightly reflected and must act as a rather efficient brace to the comb-lateral. The inner 14 marginals are unicuspid, although the base is broad, as in all of the Helicinidae.

While the description of the radula of the type species throws light on the relationships of the genus s. s., the other groups need examination. As pointed out under *Lucidella*, it is very probable that other distantly related small species have been included in the genus, as a whole. Since Chitty's description of the many species and "genera", the group seems to have received very little attention.

TABLE IV. RADULAR FORMULAE IN *Stoastoma*, *Eutrochatella*, *Viana*, AND *Calybium*.

	Centrals.			Comb	Marginals				Grand
	A	B	C	Lateral	1	2	3	Total	Total
S. pisum	1	3	4	3	14	6		53	117
E. erythraea	3	3	4	8–9	10	2	3	46	103
E. mestrei	3	3	4	8	17	5		64	139
E. jugulata	3	3	4	10	13			58	127
E. chrysochasma	3	3	4	7–9	12–14	(Troschel)		50+	111+
E. s. politula	3	3	3–4	4–5	13	5		45	101
E. pyramidalis	3	3	4	5	11			44	99
E. rupestris	0	3	2–3	0	14	5		35	81
E. sloanii	0	0	1	0	20	10		56	123
E. remota	0	0	1	0	24			80	171

[41] 1 dried specimen; A. N. S. P. no. 15236; collected in Garrett's Woods, near Mandeville, Jamaica, by A. P. Brown (1910).

	Centrals.			Comb	Marginals				Grand
	A	B	C	Lateral	1	2	3	Total	Total
E. a. columellaris	0	1	2	0	26			71	153
E. chrysostoma	0	0	0?	0	(Troschel)				
E. pulchella	0	0	1	0	40			62	135
E. tankervillii	0	0	0?	0	90+	?(Troschel)		90+	191+
E. stellata	0	0	2	0	39			104	219
E. torrei	0	0	2	0	43			111	233
V. regina	0	0	1	0	25	5	14	100	211
C. mouhoti	0	0	1	0	10	1		28	67

Genus **EUTROCHATELLA** Fisher. West Indies; Guatemala; Venezuela???

Subgenus TROSCHELVIANA new subgenus. Western Cuba.
Type *H. erythraea* "Wright" Sowerby (1866).

Section TROSCHELVIANA s. s. Western Cuba.

In this section the radulae of the type species[42], *E. mestrei*[43], and *E. jugulata*[44] have been examined. In addition, the radula of *E. chrysochasma* has been described and figured by Troschel (1856–63). As he pointed out clearly the distinctness of this group, which is almost worthy of generic separation, it is but fitting that it bear his name. The radula of *E. erythraea* is figured here (Plate VI, fig. 27) and the formulae of all four species are included in Table IV.

The paired centrals of these species have large and well-developed cusps: 3 on each A and B central and 4 on the C-central. The T-lateral, although quite similar in shape to that in the rest of the genus, bears a number of well-marked cusps on its inner edge. The accessory plate bears a stout hook, which fits over the inner branch of the stalk to the T-lateral. The unicuspid marginals are not very numerous, and bear long, sharp blades.

The shells of the species in this group are rather small, and are more elevated than in any other helicinid group. They lack the distinct spiral sculpture of the rest of the genus *Eutrochatella*. From these shell characters, I think that the following species should be included in this group:

E. alboviridis ("Wright" Pfr.) (1864).
??**E. trochulina** (d'Orbigny) (1845) Cuba. (Not the Haitian citations).
E. erythraea ("Wright" Sowerby) (1866). Type species.
H. rubella "Wright" Pfr. (1864), not of Green (1832).
E. rubella citrinocallossa A. J. Wagner (1908).
E. jugulata (Poey) (1856).
E. chrysochasma chrysochasma (Poey) (1853).

[42] 2 dried specimens; A. N. S. P. no. 14868; from Cuba; collected by Wright.
[43] 2 dried specimens; A. N. S. P. no. 98798; Mogotes de la Cerro de Cobras, Cuba; collected by J. B. Henderson (1909).
[41] 2 alcoholic specimens; from Western Cuba; sent me by J. B. Henderson.

E. chrysochasma jucunda ("Gund." Pfr.) (1863).
??**E. chrysochasma hernandezi** "Wright" A. J. Wagner (1908).
E. mestrei Arango (1878).

Section CUBAVIANA new section. W. Cuba.
Type *H. politula* Poey (1852). Santa Cruz, Cuba.

The radula of the type of this section has been described and figured by Troschel (1856–63). I have re-examined it[45] and also *E. pyramidalis*[46]; the T-lateral of the former figured (Plate VI, fig. 33). The radular formulae of both species are given in Table IV.

The centrals of this section are not quite so definitely cusped as in the preceding group, but are very similar. The T-central has only a few scallops and points near the outer edge of the margin. The A-plate, not shown by Troschel, is very similar to that in *Troschelviana* s. s.

The shells of this section are not quite so elevated as in the preceding group, but are more nearly conical in shape. They agree with it in the poor development of the spiral sculpture. I think that probably the following species belong here:

E. methfesseli (Pfr.) (1862).
E. straminea straminea (Morelet) (1851).
H. exacuta Poey (1852).
E. straminea rubromarginata ("Gund." Poey) (1856).
E. straminea festa ("Gund."Sowerby) (1866).
E. straminae nodae (Arango) (1862).
E. straminea politula (Poey) (1852). Type.
E. fuscula ("Gund."Pfr.) (1863).
E. cisnerosi (Arango) (1878).
E. wrighti wrighti (Pfr.) (1863).
??**E. wrighti xanthacme** A. J. Wagner (1911).
E. elongata (d'Orbigny) (1845).
E. pyramidalis pyramidalis (Sowerby) (1842).
E. pyramidalis percarinata A. J. Wagner (1908).
H. conica d'Orbigny (1845), not Pfr. (1839).
??**E. scopulorum** (Morelet) (1849). Isle of Pines.
H. luteopunctata Poey (1852).
H. luteoapicata Poey (1854).

Subgenus PYRGODOMUS C. and E. Cuba to Guatemala; Bahamas?

Pyrgodomus Crosse and Fischer (1893). Type (monotype) *H. chryseis* Tristram (1861). Guatemala.
Artecallosa A. J. Wagner (1908). Type (now chosen, as used as *Pyrgodomus*) *H. chryseis* Tristram (1861). Guatemala.
? *Callida* A. J. Wagner (1908). Type (by tautonomy) *H. calida* Weinland (1862) (*E. callida* A. J. W.). Not *Callida* "Dejean" Leconte (1859).[47]

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[45] 2 dried specimens; A. N. S. P. no. 15170; Rangel, Cuba.
[46] 3 dried specimens; A. N. S. P. no. 14885; southwestern Cuba.
[47] This group may belong to *Eutrochatella* s. s., but the size of the shell and its shape look more like this subgenus. I do not think the name can be used, altho *Calleida* Dejean (1825) appears to be the original spelling of the genus in Coleoptera

E. microdina microdina (Morelet) (1851). Vera Paz, Guatemala.
E. microdina chryseis (Tristram) (1861). Guatemala (may be a sex-form).
E. simpsoni Ancey (1886). Utilla Island, Bay of Honduras.[48]

Of this subgenus, I have only been able to examine *E. rupestris* (Pfr.) (1839)[49], but this species agrees quite well in shell characters with the typical, mainland species. The A-central has no definite cusps, altho its margin is slightly wavy. The B-central has three rather irregular cusps. The C-central has 2 or 3 points (Plate VI, fig. 28). The T-lateral has no definite cusps on the margin, but the horny thickenings of the umbrella-shaped cutting-edge show four or five irregular, but sharply marked folds, which gives the tooth a wavy appearance under certain lights. A. J. Wagner has described the shell characters of the group, although I doubt the inclusion of some of the larger species.

Subgenus PRIOTROCHATELSA Fischer. Isle of Pines.

Prictrochatella Fischer (1893). Type *H. constellata* Morelet (1847). Isle of Pines.

In this subgenus, the radulae of *E. stellata*[50] and *E. torrei*[51] have been examined. The radular formulae of both are given in Table IV, and that of the former is figured (Plate VI, fig. 30). The radula of this subgenus is practically the same as in *Eutrochatella* s. s., except that the R-central is broadly elliptical, instead of circular. A. J. Wagner indicates this as a primitive group, but I regard it as among the most highly specialized forms in the whole subfamily.

The operculum is superficially something like that of *Geotrochatella*, but in *Priotrochatella* the calcareous plate is dominant, while in the eastern group the horny plate is best-developed. The calcareous portion of the operculum of *Priotrochatella* is similar in texture to that of *Eutrochatella* s. s., and is not spiral but practically linear. The nucleus, which is spiral as throughout the family, is quite near the columellar margin, and the growth-lines mainly show externad. I regard it as simply a specialized condition of the *Eutrochatella*-operculum, due to the shape of the aperture.

[48] In addition, *H. exigua* Pfr. (1849), from Honduras (Dyson), may possibly belong here, but it is unrecognizable from description.
[49] 1 dried specimen; A. N. S. P. no. 15081; collected in Cuba by Poey.
[50] 1 dried specimen; A. N. S. P. no. 118935; Sierra de Caballos, I. of Pines (W. F. Clapp).
[51] 1 dried specimen; A. N. S. P. no. 15083; Isle of Pines (R. Arango). Wm. F. Clapp (1918) has described and figured the radulae of the three species of this genus.

Growth has been retarded towards the columellar wall and accentuated towards the palatal margin. This idea is substantiated by the crushed and thickened growth-lamellae along the basal and columellar margins. A. J. Wagner's figures (1905, 1907) are very diagrammatic; that of Fischer (1893), although somewhat vague, shows the fundamental structure much better. The separation of this group from *Eutrochatella* s. s., even as a subgenus, is only justifiable on the grounds of the peculiar shell and opercular characters.

Subgenus EUTROCHATELLA s. s. West Indies; Venezuela???

Section USTRONIA A. J. W. Cuba.

Ustronia A. J. Wagner (1908). Type (now chosen) *H. sloanii* d'Orbigny (1845). Cuba. (=*H. sloanei* A. J. W. and authors, not of d'Orbigny).

The radula of the type species has been figured and described by Troschel (1856–63). I have re-examined this species,[52] and have also studied *E. acuminata columellaris*[53] and *E. remota*.[54] I am unable to name any definite characters of the radula that will separate this group from the next. It appears to have a smaller number of unicuspid marginals than does *Eutrochatella* s. s. The specimen of *E. acuminata columellaris* has a minute, but very sharp-pointed cusp at the inner end of the margin of the B-central.

Section EXCAVATA A. J. Wagner. Cuba, Haiti, Jamaica.

Excavata A. J. Wagner (1907). Type (by tautonomy) *H. excavata* Pfr. (1855). Haiti.

In this section the radula of *E. chrysostoma* ("Sh." Pfr.) (1850) has been described and figured by Troschel (1856–63).

Section EUTROCHATELLA s. s. Jamaica.

Ampullina Blainville (1825). Not Saint-Fond (1803) etc. Type A. *striata* Blainville (1825).

Trochatella Swainson (1840). Type *H. pulchella* Gray (1825). Jamaica. Not *Trochatella* Lesson (1830).

Eutrochatella Fischer (1885). Type *H. pulchella* Gray.

Granifera A. J. Wagner (1907). Type *H. pulchella* Gray.

In this section the radula of the type species of the genus[55] has been examined and is figured (Plate VI, figs. 31 and 32). Troschel (1856–63) has described and figured that of *E. tankervillii* (Gray) (1825). His statement that all of the marginals are unicuspid

[52] 2 dried specimens; A. N. S. P. no. 93661; collected near Havana, Cuba, by C. F. Baker.

[53] 1 alcoholic specimen; sent me by J. B. Henderson; western Cuba.

[54] 1 alcoholic specimen; sent me by H. B. Henderson; western Cuba.

[55] 1 alcoholic specimen; A. N. S. P. no. 101221; collected near Mandeville, Jamaica, by A. P. Brown (1910), and 1 slide, in the collection of the A. N. S. P. mounted by A. P. Brown.

is doubtless erroneous. However, *Eutrochatella* does have a larger number of unicuspid marginals than does *Ustronia*, and in this features agrees better with *Priotrochatella*. Its separation from *Excavata* seems justifiable on the basis of the heavier sculpture of the shell in this typical section.

Genus **VIANA**. H. and A. Adams. Cuba.

Viana H. and A. Adams (March, 1856). Type *H. regina* Morelet (1849). Cuba.
Hapata Gray (Nov., 1856). Type *H. regina* Morelet.
Rhynchocheila Shuttleworth (1878). Type *H. regina* Morelet.

In this genus, through the kindness of Mr. J. B. Henderson, I have been able to examine the type species[56]. Before receiving his material, the laterals alone of *V. regina subunguiculata* (Poey) were obtained by washing out dermestid feces from an old shell. *V. regina* is figured (Plate VII, figs. 34, 35, 36).

The paired centrals have no definite cusps, although there is a rounded hook on the C-central. The R-central is shield-shaped with two scallops on each side, a very well-marked triangular cusp, and a rounded base. The A-central is proportionalely very large, while the B and C centrals are much smaller, and appear to be rather weak, as they are easily crushed in mounting the specimen, The T-laterals are exceptionally large (.5 mm. in diameter); each is fully as large as the whole central area (7 teeth). The stalk or base is proportionately very short and stout, while the reflecteb portion is semicircular (Plate VII, fig. 36 gives anterior view) and very large. It is less dome-shaped than in *Eutrochatella*. The accessory plate is small and, when united is almost completely hidden by the T-lateral. The unicuspid marginals are more broadly rounded at the tips than are those of *Eutrochatella* and the inner, multicuspid ones are not as deeply cleft.

In addition the shell-characters are peculiar. Especially noteworthy is the definite sinus on the outer lip of the aperture of the male. Altogether, it seems that the generic separation of this group is justifiable on natural grounds. In addition, there is a practical reason. *Viana* (and also its two synonyms) is prior to *Eutrochatella* Fischer, and would become the generic name of the entire group if the two were combined. The resemblance of Fischer's term to the original, preoccupied name, *Trochatella*, and its wide acceptance, would make this peculiarly unfortunate.

[56] 2 alcoholic specimens; Cuba from collection of J. B. Henderson.

Genus **CALYBIUM** Morelet. Indo-China.

Subgenus CALYBIUM s. s.

Calybium Morelet (1891). Type (monotype) *C. massiei* Morelet (1891).

Subgenus GEOTROCHATELLA P. Fischer.

Geotrochatella P. Fischer (1891). Type (now chosen) *H. mouhoti* Pfr. (1862).

In this group the radula of the type species *C. mouhoti* (Pfr.)[57] has been examined and is figured (Plate VI, fig. 29). It is startlingly like that of *Viana regina*, but has several, rather important differences. The A-central is not especially enlarged, as compared to the two outer, paired centrals. The unicuspid marginals are much broader, and the number of marginals is the smallest observed (28), which is remarkable when one considers that the tiny *E. rupestris* has 35. As the broad, outer marginals were observed in both radulae of *C. mouhoti*, it does not seem possible that the count is very erroneous.

With the depressed shell, *Geotrochatella* has a linear operculum, somewhat similar in shape to that of *Priotrochatella*. However, the horny plate of the operculum in the former group is well-developed, while the calcareous plate is extremely thin. The spiral nucelus is near the columellar margin. The horny plate has a thickening, which runs transversely across the inner side; when examined under the microscope, this thickening is seen to consist of lamellae, which project out a considerable angle to the rest of the plate. As the margin is not thickened, as is the calcareous plate of *Priotrochatella*, it appears as if the growth-stress, due to the shape of the aperture, finds expression in this lamellar thickening across the middle of the plate. Thus the opercula of *Priotrochatella* and *Geotrochatella*, although superficially similar, are fund mentally different, both in texture and arrangement of the growth lamellae. For this reason and on account of the divergence of the radulae, it seems that the relationship between these two groups is not as close as has often been stated. They probably represent parallel development in two rather distantly related stocks. The dominance of the horny operculum also helps to separate this group from *Viana*, which, it appears to me, is more probably its closest relative in the West Indies.

A. J. Wagner included *Geotrochatella*, *Calybium* and *Priotrochatella* in his Pseudotraochatellinae. This "subfamily," altho based on opercular characters, had for its type genus *Pseudotrochatella*

[57] 2 dried specimens; A. N. S. P. no. 66060; collected at Luang-Prabang, Laos, by Ph. Dautzenberg. (1895).

Nevil (1881) a subfossil form of which the operculum was unknown. The peculiar spiral sculpture of the embryonic shell of *Pseudotrochatella*, and its habitat, the Island of Mauritius, render its reference to the Helicinidae extremely dubious, at least until the operculum is known.

In conclusion, it may be stated that the position of the spiral nucleus of the operculum, and the arrangement of the growth-lamellae, furnish excellent characters for the separation of the minor groups. The relative dominance of the horny and calcareous plate, altho somewhat variable, especially with age, are of value, even in the separation of genera. On the other hand, the opercular characters are not of much value in the determination of the relationship between genera, and certainly cannot be used for the division of the Helicinidae into subfamilies.

Description of Plates III—VII.

On account of the considerable difference in size, the capituliform complexes are usually shown here with a different magnification than are the centrals and marginals of the same species. In addition, it was found necessary to show the radulae of different species with different degrees of magnification. For these reasons, the centrals and marginals of each species are in a group by themselves, while the capituliform complex is shown separately, usually with less magnification.

In the following descriptions, the magnification is given as 1, 2, 3, 5 or 6 times (diameters). This means that the drawing with the least magnification is taken as a standard, and the enlargement of the others is expressed in proportions to the nearest integer, so as to facilitate their rapid comparison, by the use of a simple fraction. The accurate scale in microns (μ = .001 mm.)is given with each set of figures under the same magnification. Each scale pertains to the figures between it and the next scale above, and to those below in case no other scale is given. All of the drawings were made with the aid of the camera lucida. The magnification under which the drawings were first made is as follows: ×1 = 248 diameters; ×2 is a camera lucida reduction from ×3; ×3 = 705 diameters; ×5 = 1180 diameters; ×6 = 1490 diameters.

All of the teeth in the series shown are those from the right side. As the central groups are all arranged in the same order, with the R-central at the left hand of the sheet, followed by the A, B and C centrals in order named, they are not specially numbered. The marginals are numbered as they occur in the transverse row, from the center out. The figures themselves are numbered separately at the edge of the plate. All of the teeth, including the tips of the marginals, are oriented into the most common position, although this is necessarily often only approximate.

Plate III.—*Hendersonia, Oligyra, Lucidella* and *Helicina*. Centrals and Marginals.

Fig. 1—*Hendersonia occulta*. Centrals and tips of 1rst, 8th and 13th marginals (x5).

Fig. 2—*Oligyra orbiculata*. Centrals (x5). Compare fig. 1 for marginals.

Fig. 3—*Oligyra* (*Succincta*) *flavida strebeli*. Centrals and tips of 1st, 5th, and 12th marginals (x5).

Fig. 4—*Lucidella aureola*. Centrals and tips of 1st, 6th and 40th marginals (x6) (A-central shown below in tilted position).

Fig. 5—*Lucidella* (*Poenia*) *lirata*. Centrals (x6). Compare 4 for marginals.
Fig. 6—*Helicina neritella*. Centrals (in row instead of in the more common position); tip and inner view of 4th marginal; a, b, c: tips of marginals further out (exact position unknown); d: edge view of distal end of a marginal to show sickle-shaped tip. (x3).
Fig. 7—*Helicina* (*Tenuis*) *tenuis*. Centrals and tips of 1st, 5th, and 12th marginals (x3).
Fig. 8—*Helicina* (*Oxyrhombus*) *amoena*. Centrals and tips of 1st, 3rd and 9th marginals (x3).
Fig. 9—*Helicina* (*Tristramia*) *zephyrina*. Centrals and tips of 1st, 3rd, 6th and 12th marginals; outer view of 2nd; inner view of 7th; edge view of distal end of 17th ;and edge view of proximal end of 8th to show U-shape of base. (x3)

Plate IV.—*Hendersonia, Oligyra, Helicina* and *Schasicheila*. Capituliform Complexes.

Fig. 10—*Hendersonia occulta*. Comb-lateral and accessory plate separated (x3).
Fig. 11—*Oligyra orbiculata*. Comb-lateral and accessory plate separated. (x3).
Fig. 12—*Oligyra* (*Succincta*) *flavida strebeli*. Comb-lateral and accessory plate united (x3).
Fig. 13—*Helicina* (*Tristramia*) *zephyrina*. Comb-lateral and inner end of accessory plate united (x3).
Fig. 14—*Helicina* (*Tenuis*) *tenuis*. Comb-lateral and accessory plate separated (x3).
Fig. 15—*Helicina* (*Oxyrhombus*) *amoena*. Comb-lateral and accessory plate separated (x3).
Fig. 16—*Schasicheila* (*Emoda*) *silacea*. Comb-lateral and accessory plate separated (x3).
Fig. 17—*Helicina neritella*. Comb-lateral and accessory plate separated. (x3) a. cusp-bearing portion of comb-lateral. b. handle or base of comb-lateral. c. triangular outer projection of comb-lateral; this forms a support for: d. continuation of cusp-bearing portion. e. depression and thinning of comb-lateral (shown by dotted lines); on opposite side from that viewed. This is for the reception of the base of the comb-lateral next anteriad (above in figures). f. Portion of accessory plate which fits under the triangular projection of the comb-lateral(c). g. lanceolate appendix of the accessory plate. h. reflected portion, which invests the outer end of(d). x. termination of each piece (when united in natural position) marked on the other.
17A—*Helicina adspersa*. Comb-lateral and accessory plate, slightly separated (x3).

Plate V.—*Schasicheila, Lucidella, Aphanoconia*, and *Oligyra*. Radulae.

Fig. 18—*Schasicheila hidalgoana*. Centrals and tips of 1st, 4th, 12th and 21rst marginals. (x5).
Fig. 19—*Schasicheila* (*Emoda*) *silacea*. Centrals and tips of 1st, 4th, and 12th marginals (x3).
Fig. 20—*Schasicheila hidalgoana*. Capituliform complex united (x3).
Fig. 21—*Lucidella* (*Poenia*) *lirata*. Capituliform complex united (x6).
Fig. 22—*Lucidella aureola*. Capituliform complex united (x6).
Fig. 23—*Aphanoconia* (*Sphaeroconia*)*v erecunda*. Central sand tip of 1st marginal (x5). Comb-lateral and accessory plate separated (x3).
Fig. 24—*Oligyra* (*Succinta*) *oweniana coccinostoma*. Centrals and tips of 1st, 3rd, 7th, and 12th marginals, and edge view of distal end of 4th to show wings (x5). Comb-lateral and accessory plate separated (x3).

Fig. 25—*Oligyra* (*Alcadia*) *palliata*. Centrals and tips of 1st, 3rd, and 15th marginals (x5). Comb-lateral and accessory plate separated (x3).

Plate VI. *Stoastoma*, *Eutrochatella*, and *Calybium*. Radulae.

Fig. 26—*Stoastoma pisum*. Centrals, and 1st and 11th marginals, and tip of 18th; comb-lateral and accessory plate separated (x5).

Fig. 27—*Eutrochatella* (*Troschelviana*) *erythraea*. Centrals, and tips of 1st. 5th, and 17th marginals; T-lateral and accessory plate separated (x5).

Fig. 28—*Eutrochatella* (*Pyrgodomus*) *rupestris*. Centrals; T-lateral and accessory plate separated (x5). For marginals, see fig. 27.

Fig. 29—*Calybium* (*Geotrochatella*) *mouhoti*. Centrals and tips of 1st, 5th, 11th and 12th marginals; T-lateral and accessory plate (below) separated (x3).

Fig. 30—*Eutrochatella* (*Priotrochatella*) *stellata*. Centrals and tips of 1st, 5th, 10th, 40th and 50th marginals; T-lateral and accessory plate united (x3).

Fig. 31—*Eutrochatella pulchella*. Centrals (x3). See 30 for marginals.

Fig. 32—*Eutrochatella pulchella*. T-lateral and accessory plate united (x1+).

Fig. 33—*Eutrochatella* (*Cubaviana*) *politula*. T-lateral and accessory plate united (x3).

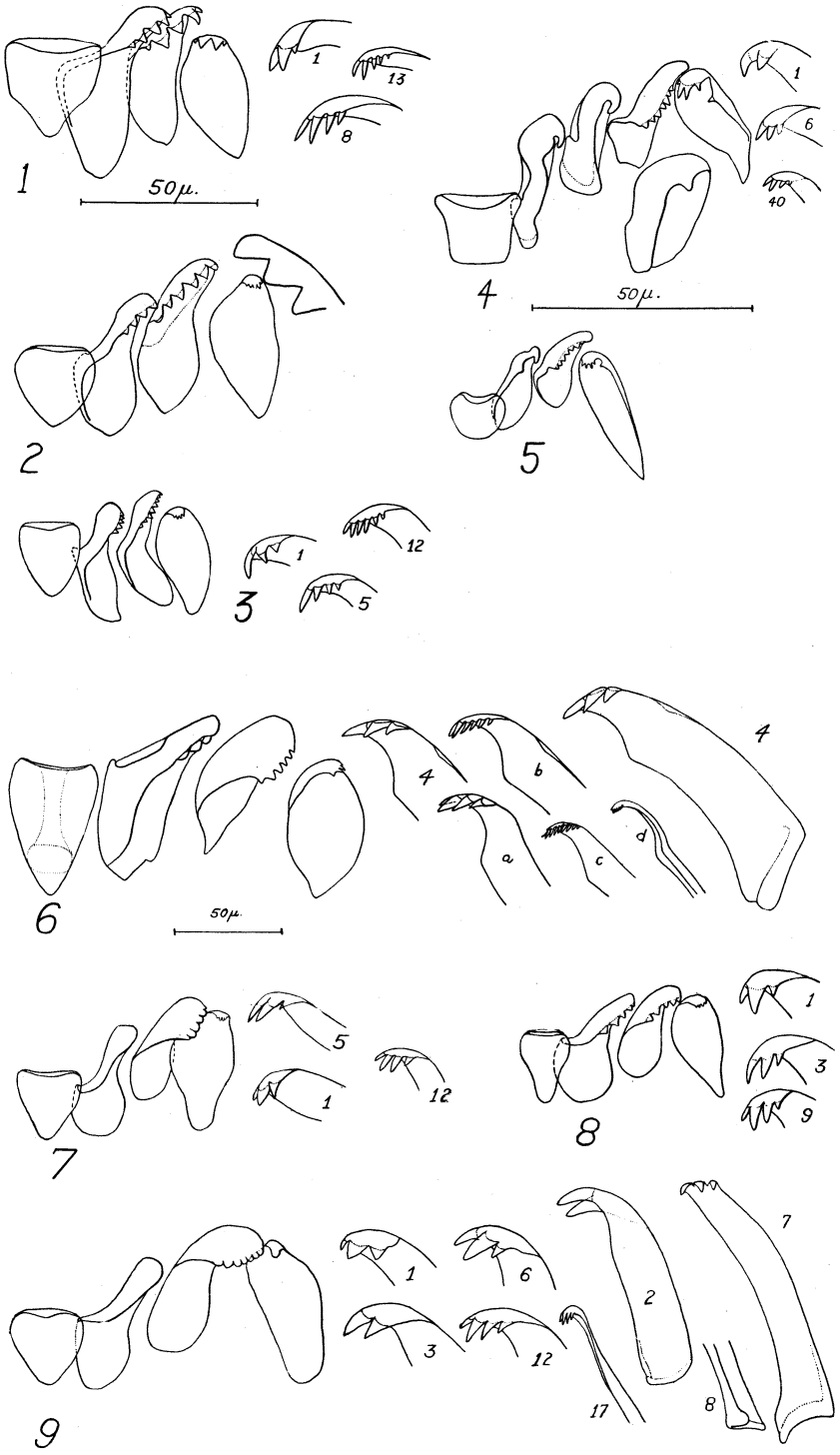
Plate VII. *Viana* and *Helicina*.

Fig. 34—*Viana regina*. Centrals, capituliform complex and separated accessory plate (x1+).

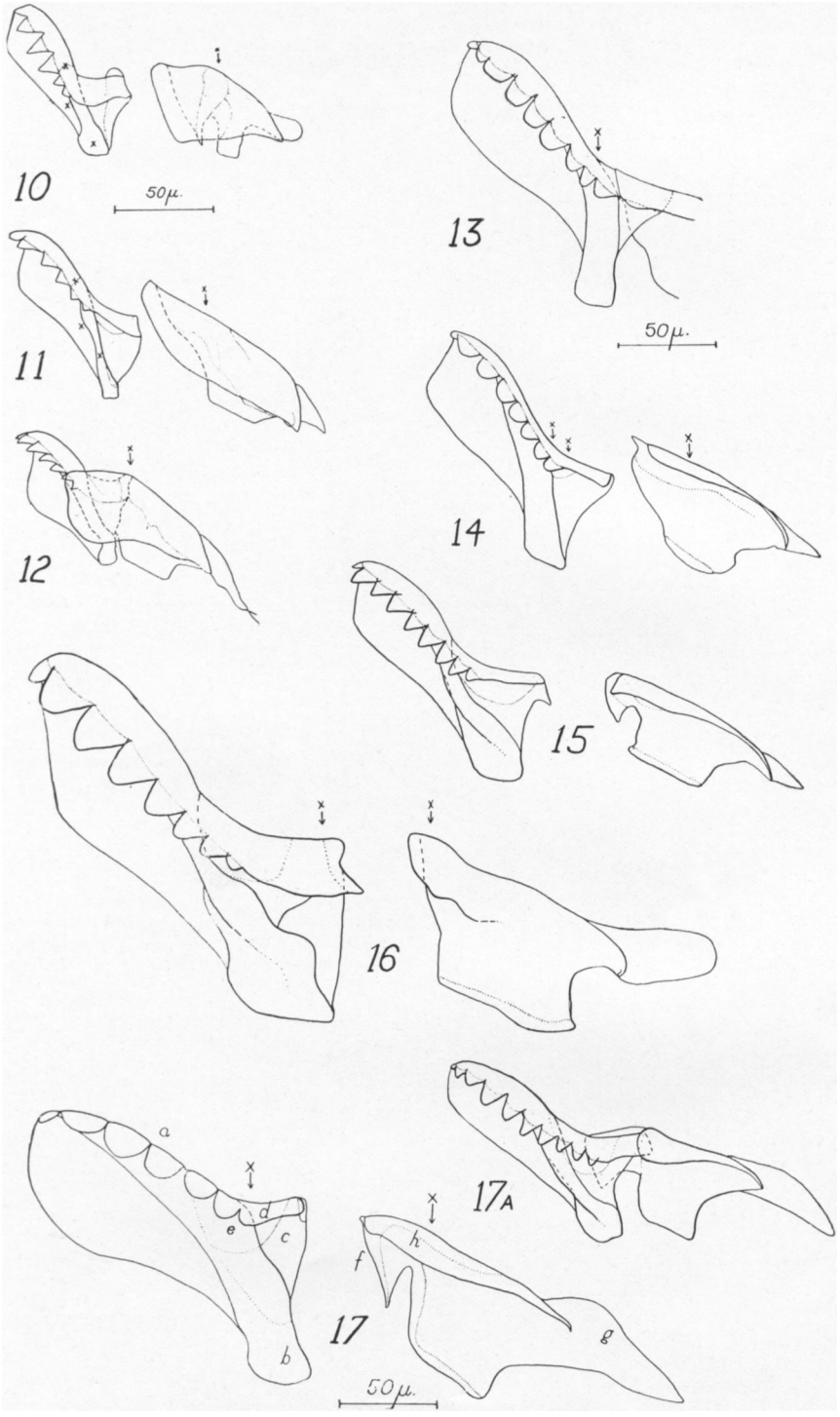
Fig. 35—*Viana regina*. Centrals, and tips of 1st, 10th, 16th, 26th, and 30th marginals (x3).

Fig. 36—*Viana regina subunguiculata*. Anterior view of T-lateral, to show outline of reflected portion (x½).

Fig. 37—*Helicina adspersa* (small form *marmorata*). Centrals, 2nd marginal and edge of 4th marginal (x5).



BAKER: RADULA OF HELICINIDAE.



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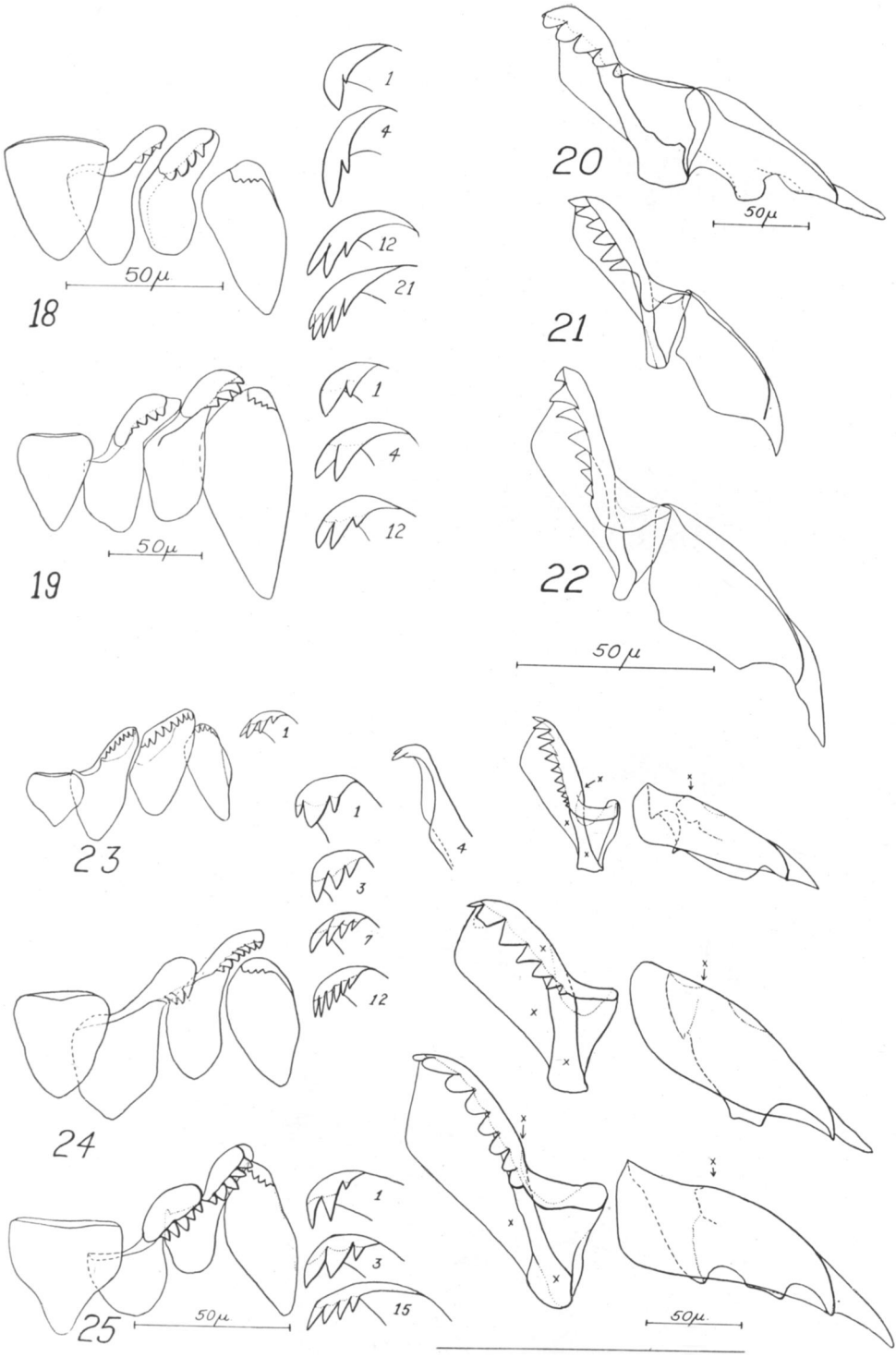

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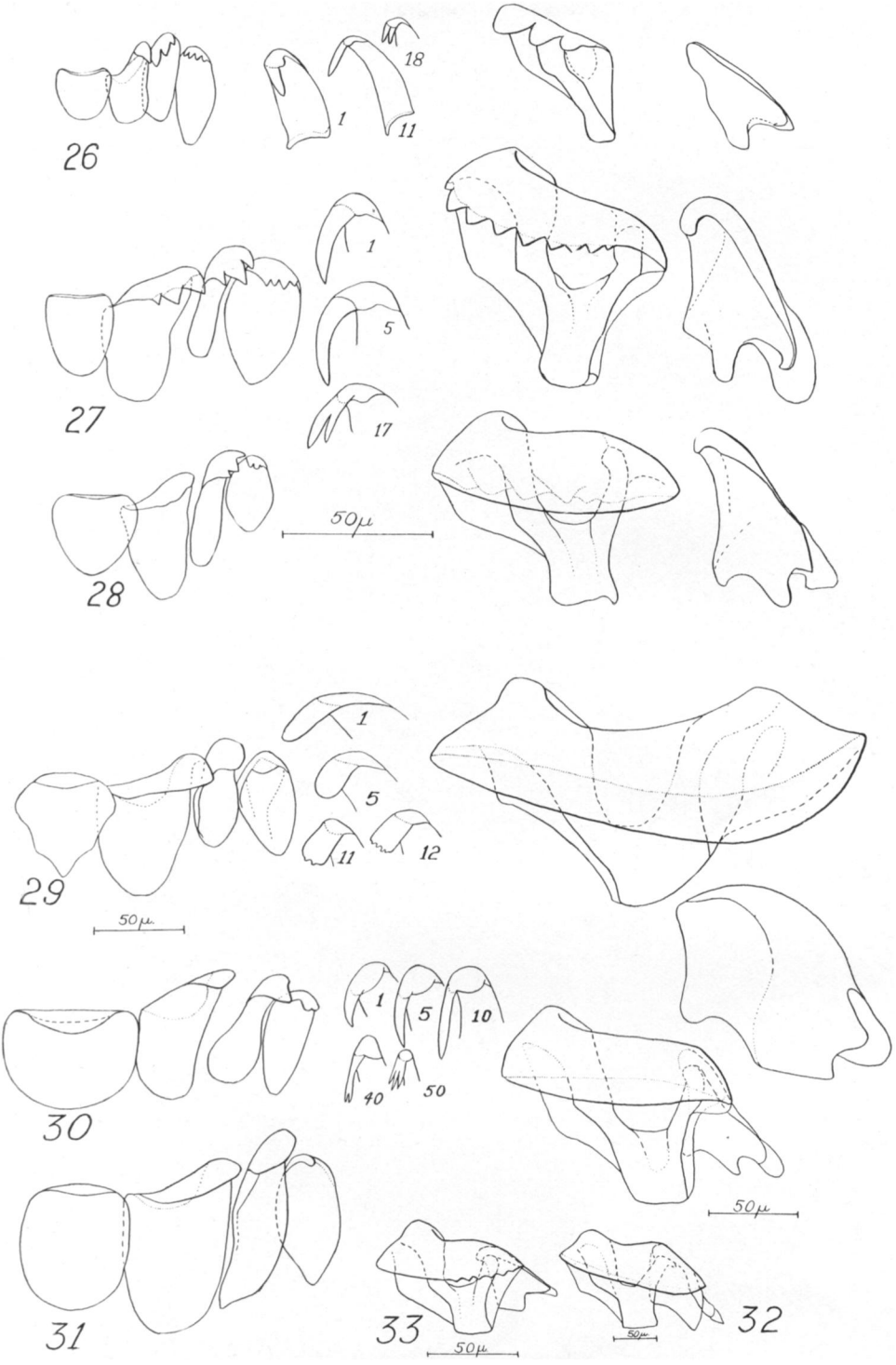

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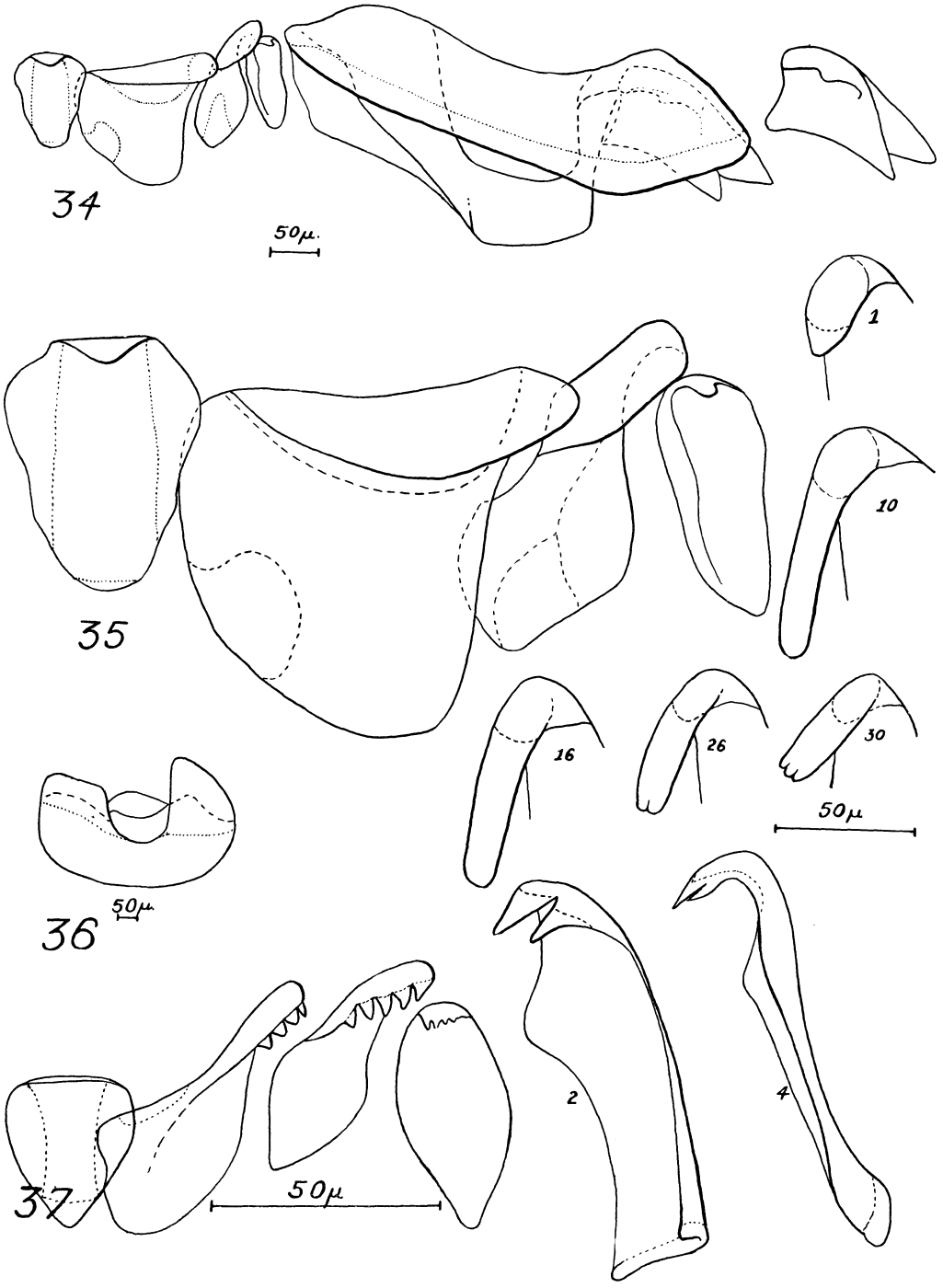

BAKER: RADULA OF HELICINIDAE.